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GENETICS

PERIODICAL RECORD OF INVESTIGATIONS
BEARING ON HEREDITY AND
VARIATION

~~NOVEMBER~~, 1917

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Princeton, New Jersey

GENETICS

A Periodical Record of Investigations Bearing on
Heredity and Variation

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CORRIGENDA

ge 49, first formula, for numerator, instead of " $\Sigma(yE)/N=\bar{y}\bar{E}$," read " $\Sigma(yE)/N=\bar{y}\bar{E}$ ".

ge 50, first formula, for " $E = (\bar{E} - r \frac{\sigma_E}{\sigma_y})\bar{y} + r \frac{\sigma_E}{\sigma_y}y$ " read " $E = (\bar{E} - r \frac{\sigma_E}{\sigma_y}\bar{y}) + r \frac{\sigma_E}{\sigma_y}y$ ".

ge 60, fourth formula from bottom, numerator, for

" $r_{ye_1} - r_{ye_2} r_{e_1e_2}$ " read " $r_{ye_1} - r_{ye_1e_2} r_{e_1e_2}$ ".

ge 99, fifth line of footnote, for "SEWELL WRIGHT", read "SEWALL WRIGHT".

ge 99, last line of footnote, for " $B_n F_{n-1} G_{n-1}$ " read " $B_n - F_{n-1} - G_{n-1}$ ".

ge 117, interchange lines 18 and 19, placing "in sections (12), (13) and (14)" above the preceding line.

ge 144, fourth line from bottom, for " $2p(p+q+t)+qs+pt$ " read " $2q(p+q+t)+qs+pt$ ".

ge 146, last line, for " $(r+1)(p+q)(p+q+s+t)$ " read " $(r+1)(p+q)(p+q+2s+2t)$ ".

ge 154, near middle, first expression in "Column 1" of table, for " $\frac{2^{n-1}+1}{2^{n-1}} + \tau^n$ " read " $\frac{2^{n-1}-1}{2^{n-1}} + \tau^n$ ".

ge 17, legend of fig. 3, for "*pycuella*" read "*pycnella*".

ge 17, table 1, last line of third section, Ear No., for "(96-6)-4-1-6-8" read "(69-6)-4-1-6-8".

ge 18, line 13, for " ± 0.143 " read " ± 0.119 ".

ge 28, line 28, for "38 few seeds striped" read "28 few seeds striped".

ge 29, line 29, for "254" read "244" and ratio per 4, for "3.107 : 0.893" read "3.079 : 0.921".

ge 30, line 30, for "0.107" read "0.079".

ge 31, line 31, for " ± 0.065 " read " ± 0.075 ".

ge 70, table 2, first line below heading, for " $| 21 | 71 | 8$ " read " $| 19 | 72 | 9$ ".

ge 70, table 2, third line from bottom, for " $| - | 79 | 21$ " read " $| 3 | 76 | 21$ ".

CORRIGENDA (Continued)

Page 274, line 6, for "324" read "824".

line 25, for "445" read "446".

line 28, for "40.4" read "42.4".

last line, for "1.220 : 2.771" read "1.225 : 2.775".

Page 279, line 24, for "36" read "30".

line 25, for "58" read "64", and for "2" read "3".

line 26, for "4" read "2".

Page 329, for lines 11-14 substitute the following:

"quence (rel. freq.) of the mating. For example 3 out of fathers are very tall; if such married very tall women proportionally, then 3 out of 50 choices of such women should be made by very tall men; actually $8.4 = 3 \times 2.8$ is the proportion; where 2.8 is the preference factor".

Page 330, table A, second column, totals, for "137" read "50"; fifth column, first entry, for "2.9" read "2.8", and fifth entry, "1.0" read "0.1".

Page 379, line 16, for "nals, all males, and about 132 cm tall" read "mother, approximately 106 cm tall".

Pages 388, 389. The following citations should have been included:

CUSHING, H., 1911 *Dyspituitarism*. Harvey Lectures 1910-11 pp. 31-
New York: Lippincott.

DALF, H II, 1915 The physiology of the thyroid gland *The Practitioner*
94: 16-25.

DOCK, G., 1915 The pituitary body and other glands of internal secretion
Modern Medicine, ed. by W. Osler and T. McCrae 4: 804.

PLATE, L., 1913 Vererbungslehre mit besonderer Berücksichtigung des Menschen, für Studierende, Ärzte und Züchter. pp. xii + 519. Leipzig: Wilhelm Engelmann.

PREUSS, J D E, 1832-1834 Friedrich der Grosse. Eine Lebensgeschichte
5 vols. Berlin: Nauck.

WEINBERG, W., 1912 Zur Vererbung des Zwergwuchses *Arch. f. Rassengesell.- Biol.* 9: 710-717.

Page 394, line 17, for "are" read "is".

Page 397, fifth formula under F_2 in class 1, for "ggHh" read "ggHH".

Page 398, line 18, for "4, 5 and 6" read "4 and 5".

Page 416, omit line 27, "1917 Genetical studies etc."

Page 439, middle of page, section heading, for "MATIGS" read "MATINGS".

Page 469, line 29, for "types" read "type".

Page 472, line 27, for "6 factors" read "9 factors".

Page 475, table 3, heading for "chromsomes" read "chromosome".

Page 504, line 6, for "Limit" read "Limit".
 $n =$ $n = \infty$



Yours affectionately
Francis Galtton

FRONTISPIECE—SIR FRANCIS GALTON

FRANCIS GALTON was born at "The Larches" in Sparksbrook, Birmingham, England, February 16, 1822, and died January 17, 1911. A precocious child, grandson of ERASMUS DARWIN by his second wife, and thus a half first cousin of Sir CHARLES DARWIN, heir to a fortune adequate to support him comfortably without dependence upon his own earning capacity, and handicapped by frequent and serious illness, GALTON strikingly illustrated by his own career the truth of his view that mental qualities are mostly innate and little affected by education and environment. He made distinguished contributions in several fields of science,—geography, meteorology, anthropometry, experimental psychology, statistical theory, and genetics. Although he began his work in biological fields relatively late in life, his achievements have been truly epoch-making. His initial paper in this field was "Hereditary talent and character," published in *Macmillans Magazine* in 1865. His more important publications in the field of anthropometry, statistical theory, variation and heredity were "Hereditary genius" (1869), "English men of science, their nature and nurture" (1874), "Human faculty" (1883), "Life history album" (1884), "Record of family faculties" (1884), "Natural inheritance" (1889), "Finger prints" (1893), "Finger print directory" (1895), "Noteworthy families" (1906). He also published more than one hundred memoirs dealing with his investigations in blood transfusion in rabbits, heredity in man (stature, eye color, temper), heredity in sweet peas, in moths, and in Basset hounds; with anthropometry and the development of statistical theory and method and their application to problems of heredity and eugenics.

His influence on science in general and on genetics in particular can not, however, be measured by the extent of his own writings merely. FRANCIS GALTON was throughout his long life an able and active executive. His family, his financial independence, and his scientific position gained by early and important African exploration, gave him free contact with the influential men of his day, and his gentle but powerful influence was potent in many important movements. To instance only activities related to anthropometry and genetics, he founded an anthropometric laboratory in 1882, the BIOMETRIC LABORATORY in 1894 (so-named in 1900 when the journal "*Biometrika*" was established), originated the eugenics movement in 1901, establishing in 1904 an "EUGENICS OFFICE" which was later (1907) transformed into the EUGENICS LABORATORY in association with the BIOMETRIC LABORATORY at UNIVERSITY COLLEGE, London. At his death he bequeathed his residuary estate, amounting to about £45000, to the UNIVERSITY OF LONDON to found

SIR FRANCIS GALTON

the GALTON PROFESSORSHIP OF EUGENICS and to endow the FRANCIS GALTON LABORATORY FOR NATIONAL EUGENICS.

Unlike the work of MENDEL, GALTON'S work received the highest contemporary recognition and he received many honors, among which may be mentioned six medals from the ROYAL GEOGRAPHICAL SOCIETY, the ROYAL SOCIETY, the ANTHROPOLOGICAL INSTITUTE, and the LINNEAN SOCIETY, and the honorary degrees of D.Sc. from CAMBRIDGE and D.C.L. from OXFORD.

He became a Fellow of the ROYAL SOCIETY in 1856 and was a Member of its Council for four periods of one to two years each; a member of the ROYAL GEOGRAPHICAL SOCIETY (1853) and for many years a member of its Council; three time Sectional President of the BRITISH ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE,—Geography 1872, Anthropology 1877, 1885,—General Secretary 1863-1867, and twice declined the Presidency; a member of the METEOROLOGICAL COMMITTEE; Chairman of the KEW OBSERVATORY COMMITTEE; President of the ANTHROPOLOGICAL INSTITUTE; Rede Lecturer at CAMBRIDGE 1884, and Herbert Spencer Lecturer at OXFORD 1907.

The diversity of the honors conferred upon him bears testimony to the intellectual versatility of the man and to the power of his personality. His "Memories of my life," published in 1908, furnishes not merely a charmingly written account of his own life activities, but affords the thoughtful reader some insight into the great advance of science during the life of one individual. Summing up FRANCIS GALTON'S own work in a single phrase, his greatest contribution to science during his long life was his influence for the quantification of method. This influence is nowise diminishing with the lapse of time, and must long be felt in many fields of scientific activity.

A comprehensive biography, one volume of which appeared in 1914 from the Cambridge University Press, is in preparation by Professor KARL PEARSON, the first incumbent of the GALTON PROFESSORSHIP OF EUGENICS.

The portrait here reproduced was one of the last works of CHARLES WELLINGTON FURZE (1844-1904), who achieved in his brief life a high place among British portrait painters. A copy by CARTER is hung in Trinity Hall, CAMBRIDGE. The original is in the possession of Sir FRANCIS GALTON'S nephew, E. WHEELER GALTON, Esq., Claverdon Leys, Warwick, England, who has kindly given his consent to its reproduction in GENETICS.

GENETICS is indebted to Mr. W. E. D. STOKES, well known horsebreeder, of New York City, and author of "*The right to be well born*," for generously providing the funds required for the reproduction of this portrait.

GENETICAL STUDIES OF VARIEGATED PERICARP IN MAIZE¹

R. A. EMERSON
Cornell University, Ithaca, N. Y.

[Received July 24, 1916]

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PREVIOUS STUDIES

Two years ago there were presented some results of a study of the inheritance of self pattern in the pericarp of maize seeds, occurring as a sporophytic² variation in variegated ears (EMERSON 1914). Further results, in entire accord with those previously reported, have now been obtained. In addition, data bearing upon new phases of the problem are also available.

The chief results reported in the earlier paper were the following: (1) The more nearly self-colored the pericarp of any seed of a variegated ear, the more likely is the progeny of that seed to produce a self-colored

¹ Paper No. 55, Department of Plant Breeding, Cornell University, Ithaca, N. Y. Most of the data here reported were obtained in connection with heredity studies conducted at the Nebraska Agricultural Experiment Station and supported by funds of that institution.

² This change has heretofore been termed somatic variation because first manifested in somatic cells. As was apparent from the start, however, the factorial modification responsible for the visible change must often occur in meristematic cells from which later arise the germ cells as well as the somatic tissues of the pericarp or even of the whole ear. Since such meristematic cells—progenitors of epidermal tissue being excluded—are germinal rather than somatic, the variation is better termed sporophytic.

ear and the less likely to produce a variegated or colorless one. (2) Self-colored ears so produced behave as if they were F_1 hybrids between self-colored and variegated or between self-colored and colorless races, depending upon whether the variegated parent ear was homozygous or heterozygous for pericarp color and upon whether it had been self- or cross-pollinated. (3) Self-colored ears also occur occasionally with the normal variegated ears in F_1 of a cross produced by pollinating a colorless race with pollen from a variegated race; and these F_1 red ears always behave in later generations as if they were hybrids between self-colored and colorless races.

As a possible interpretation of these results, I have suggested (1) that a Mendelian factor for variegation, V , is changed to a self-color factor, S , in a meristematic cell, (2) that all pericarp cells directly descended from this modified cell develop color, (3) that of the female gametes arising from such modified cells at least one-half carry the S factor in place of the V factor, and (4) that a similar factorial change is responsible for the occasional occurrence of male gametes bearing S instead of V . It was also noted in the former paper that a certain dark variegation occurring in association with a self-colored cob spot was apparently not inherited, but that, nevertheless, distinctly different types of variegation exist in an apparently homozygous condition in different strains of maize.

MATERIALS AND METHODS, SOURCES OF ERROR

Most of the data reported in my first paper were obtained from self-pollinated ears. As was there pointed out, such data are not wholly reliable for the reason that factorial changes influencing the male gametes are never detected in the staminate inflorescence. Assurance that the pollen is not carrying a factor for self color is to be had only when pollen from colorless races is employed. In all the work done since the earlier publication, therefore, seeds have been selected only from variegated ears that had been pollinated by races with colorless pericarp.

Since on the great majority of variegated ears only a few self-colored or nearly self-colored seeds occur, and since variegated ears with a considerable number of such seeds are rare, a large number of ears must be crossed in order to get a sufficient number of self-colored seeds to afford reliable indications. To hand-pollinate a sufficient number of ears for this purpose was found impracticable owing to the short period during which the work could be done and the considerable amount of time necessarily devoted to pollination in connection with other maize studies. Cross-pollination was therefore effected by detasseling all

plants grown from variegated seed and allowing them to be pollinated naturally from colorless races grown in alternate rows. The plan followed was to examine all the plants once every day and to remove all tassels as soon as they began to show above the sheaths. This work was done by careful assistants under my direction throughout the blossoming period.

In work conducted in this way, two sources of error should be noted: (1) There is a chance that a few tassels may be overlooked until after they have begun to shed pollen. (2) A few of the pollinizers may not be colorless. As to the first of these, it can be said that no open anthers were found on any tassel of the detasseled rows and that therefore, even if such occurred, the error introduced by them was probably not greater than would have resulted from the accidental entrance of foreign pollen in guarded hand-pollination.

The second source of error, on the other hand, was positively demonstrated. Of about 1000 plants in the pollinizer rows, a single plant had self red ears. Owing to the extremely unfavorable season (1913) numerous plants with fairly well developed tassels failed to produce ears. Unfortunately, therefore, it cannot be said that the single red-eared plant observed was the only one of the sort present. In fact there is reason to believe that it was not the only off-type plant present by accident, as will appear shortly. Since there was almost no chance that the colorless seeds planted could have contained any colored seeds or that such seeds were accidentally scattered in the field, it is probable that the red-eared plant was due to an accidental admixture of pollen when the parent ear was hand-pollinated the summer before.

If hand-pollination had been practiced in this investigation and pollen accidentally taken from a red-eared plant, the ears so crossed could have been discarded. In open pollination, however, it obviously could not be determined which ears had received pollen from the off-type plant. Unfortunately, I may add carelessly, the detasseled rows were harvested before the pollinizers were and consequently before the red-eared plant was discovered. It was, therefore, impossible even to discard seed ears grown near the red-eared plant.

The only method of determining how serious such accidental admixture of pollen might be was to grow progenies of colorless ears from the pollinizer rows. In order that this test might give a fair indication of the amount of off-type pollen, numerous colorless ears were taken at random from each pollinizer row and about twenty seeds from each ear were planted in 1914. In all 134 such colorless parent ears were

represented in the planting. Owing to poor germination only 1239 plants resulted. Of these one plant had self-colored ears and five had variegated ears—an error due to off-type pollen of about one half of one percent. The five variegated ears could not have come from pollen of the one red-eared plant observed, for the progeny of this plant had only self-colored and colorless ears. Pollen carrying the variegation factor must therefore have come from some other plant or plants in the pollinizer rows or from the detasseled rows. The percentage of error is so small, however, that it need occasion little difficulty.

Many of the pollinizers that were colorless with respect to pericarp had self red cobs. This fact introduces a difficulty in connection with a study of the inheritance of a peculiar form of dark variegation associated with red cob color. The matter will be considered in its appropriate place later.

TYPES OF SEED COLOR AND OF EAR COLOR

From every variegated ear used in the next season's planting, seeds of as many types of pericarp color as possible were chosen. Each type from each ear was planted separately. Almost no wholly self-colored seeds were found. In practically all cases the most nearly self-colored seeds had colorless or extremely light colored crowns. These light crowns appear as if made up of very narrow light streaks extending from part way down the side of the seeds opposite the germ up to and converging at the point of attachment of the silks to form irregular light spots (figures 1 and 2 B). Even when these grains occurred in large patches on "freak" ears, almost no wholly self-colored seeds appeared. The cob color under such "near self" seeds, whether they occurred singly or in patches of considerable size, was rarely prominently different from that of the remainder of the ear. That is, the cobs were, as a rule, variegated throughout. Under patches of near self seeds, the color of the cob was ordinarily only slightly darker than elsewhere, the change being due to a somewhat uniform development of color at the base of the glumes (figure 3 C, D).

In addition to numerous fine and often somewhat indistinct longitudinal lines of color characteristic of most variegated maize seeds, some seeds have one or more sharply defined and deeply colored stripes (figure 4). A single stripe may cover anywhere from perhaps one twenty-fifth to nine-tenths, or more, of the seed. The stripe is always self-colored, not broken by lighter variegations. Seeds in which these self-colored stripes cover from above 50 percent to 90 percent, or more,



FIGURE 1.—Very light variegated type of maize with one normal ear (left) and one “freak” ear (right), the latter made up of self-colored and near self seeds except for three very light variegated ones near the shank. Note also the striped husks. From photograph by W. I. FISHER.

FIGURE 2.—Types of maize seeds, crown (left), germ side (middle), and side opposite germ (right). A, self-colored, B, near self, C, dark-crown variegated, D, very light variegated. Note the similarity in color pattern of B and C. From drawings by C. W. REDWOOD.

of the area, are classed together as “more than half self” (figure 4 B). Similarly seeds with a stripe covering from about 10 percent to somewhat less than 50 percent are designated as “less than half self” (figure 4 C).

The next most highly colored seeds are known as “dark-crown variegated.” These are usually rather evenly variegated, with dark crowns. On all sides of the seed there is usually a rather prominent light red color (brown in some strains) forming a background for the fine lines of darker color that make up the variegation. On the side of the seed opposite the germ are prominent stripes that converge at the point of attachment of the silks to form an irregular, dark crown spot (figures

2 C and 4 D). These dark-crown seeds are almost the exact reverse of the "near self" seeds described above, in that the light pattern of one is the counterpart of the dark pattern of the other. These dark-crown variegated seeds almost if not quite universally occur above a self-colored (red or brownish) spot of the cob. This is apparently equally true whether these seeds occur singly or in "freak" patches. In the latter case the exact correspondence in outline between cob and seed patches is most striking (figure 3 A, B). This is the only type of variegation that is commonly thus associated with dark color in the cob. In earlier statements (EMERSON 1913, 1914), I have spoken of an association between self-colored or near self seeds and self-colored cob spots, but I now believe that such an association is rarely if ever found.

Most variegated maize seeds lack the dark crown spot of seeds of the

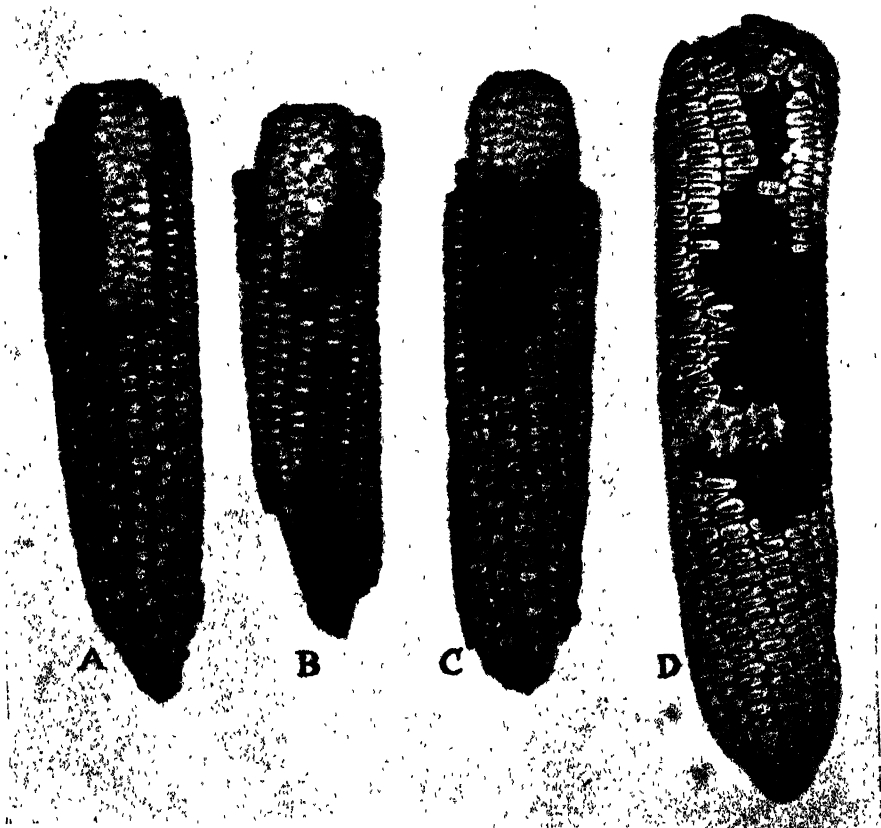


FIGURE 3.—Medium (A, C) and very light (B, D) variegated ears with "freak patches" of dark-crown (A, B) and near self (C, D) seeds. Note the association of self-colored cob spots with patches of dark-crown seeds. From photograph by W. I. FISHER.

dark-crown variegated type described above, and usually also show little or none of the light red (or brown) background noted in connection with that type. Such seeds are here known as "medium variegated" (figure 4 E). A still lighter type is distinguished as "light variegated" (figure 4 F). These differ from medium variegated seeds in degree only. They have fewer of the dark lines forming the variegation.

Still another class is known as "very light variegated." Except for occasional very narrow longitudinal lines, these seeds are almost colorless (figure 4 G). While such seeds are found occasionally on medium variegated ears, they are characteristic of certain strains of variegated maize. At a distance the ears of these strains appear colorless. Most of the seeds, however, have from one to several minute streaks or specks of color. Very light variegated ears often contain a few seeds with wholly colorless pericarp (figure 4 H).

The classes of ears are similar in part to the classes of seeds described above. Thus, I have recognized self-colored, dark, medium, light, and very light, variegated, and colorless, ears. Self-colored ears (red or brown) unlike the self and near self seeds of the variegated ears, always (so far as I have observed) have self-colored (red or brownish) cobs. In certain families a number of almost wholly self-colored ears have been observed. They are exactly like the self-colored ears in seed and cob color except that from one to at the most four or five scattered seeds are distinctly variegated. Such ears are not to be confused with the "near self" seeds described above, for their seeds, except for the very few variegated ones, are wholly self-colored. They never show the light or colorless crown spots of near self seeds. Only one ear composed almost wholly of near self seeds has ever been observed by me, and it was doubtless a "freak" ear in which the patch of near self seeds extended over nearly the whole ear instead of being confined to a smaller patch associated in the usual way with variegated grains. The ear in question not only had a light variegated cob but was borne on the same stalk with an ordinary light variegated ear (figure 1).

Ears the individual seeds of which are, throughout, say a quarter or a half self-colored, are never seen. Dark-crown variegated ears, composed wholly of dark-crown seeds, are rarely found. The three or four observed have had wholly self-colored (red) cobs. They are, I believe, to be regarded as "freak" ears, in which the patch of dark-crown seeds happened to extend over the entire ear. One such ear has been found on the same stalk with a medium variegated ear, the latter having as usual a variegated cob.



FIGURE 4.—Types of maize seeds selected from variegated ears for planting, as indicated in tables 1 and 3. A, self-colored and near self, B, more than half self, C, less than half self, D, dark-crown variegated, E, medium variegated, F, light variegated, G, very light variegated, H, colorless. From drawing by C. W. REDWOOD.

Medium variegated ears, composed in the main of medium variegated seeds but usually with scattered half self, quarter self, near self, or dark-crown seeds, and rarely freak patches of near self or dark-crown seeds, are very common (figure 3 A, C). If homozygous for variegated pericarp, they apparently always have variegated cobs. When crossed with strains having colorless pericarp and self red cobs, the resulting F_1 ears are variegated with red cobs and in F_2 all the variegated ears with red cobs are heterozygous and all with variegated cobs are homozygous for both pericarp and cob colors. Light variegated ears are like the above except that most of their grains are light variegated. Just as with medium and light variegated seeds, no sharp line of demarkation exists between medium and light variegated ears. While some ears are clearly much lighter than others, numerous intermediates are usually found in the same lots.

Very light variegated ears are composed mostly of very light variegated and colorless seeds. They rarely produce self-colored, near self, or dark-crown seeds, and I have observed among them only a few "freak" ears with large patches of dark-crown or near self seeds (figure 3 B, D). In this respect they differ notably from medium variegated ears. Their cobs are very light variegated or nearly colorless, except, as in the case of medium variegated ears, when they have been crossed with colorless-seeded, red-cobbed types, in which case all heterozygous ears have red cobs. Some apparently wholly colorless ears have been observed in strains of very light variegated maize and are doubtless to be regarded as an extreme expression of this type of variegation. Self-pollinated seeds of one such ear were found to yield a progeny consisting mainly of very light variegated ears. Very light variegation is recessive to medium variegation, as will be shown later, and the two types segregate rather sharply in F_2 .

INHERITANCE OF SPOROPHYTIC MUTATIONS FROM VARIEGATION TO SELF COLOR

The variegated ears, cross-pollinated by plants with colorless pericarp, as noted earlier in this paper, may be divided into two general lots, one of which was homozygous with respect to pericarp color and the other of which was heterozygous from having been crossed with colorless maize the previous generation. A part of the homozygous variegated lot was in reality heterozygous for medium and very light variegation.

Of the lot that was heterozygous for variegated pericarp, seeds of various color types were selected from seventy-five parent ears, and

progenies totaling 1140 plants were grown. Since we are here concerned with the inheritance of self color as contrasted with variegation, all the variegated ears will be lumped together without respect to the type of variegation. The numbers of self-colored, variegated, and colorless ears produced by the various types of seeds are given in table 1.

Since the parent ears were heterozygous for pericarp color and were cross-pollinated by colorless maize, fifty percent of the progeny of each class of seeds should have been colorless. The percentages of plants with colorless ears actually observed ranged from a little less than 46 to a little over 62. The percentage of colorless ears in the lot as a whole was 50.96. It seems likely that the individual deviations from the expected 50 percent are without significance. There is certainly no regular tendency toward either an increase or a decrease in the percentage of colorless ears from the self-colored seed to the lighter variegated seed. It can be concluded therefore that these data afford no evidence of any effect of the amount of color in the seeds of heterozygous variegated ears upon the relative numbers of colored and colorless offspring.

The things that stand out most prominently in these results are, (1) the direct relation between the amount of self color in the seeds planted and the percentage of plants with self-colored ears in the progenies in the first three classes; (2) the lack of any such relation between the amount of color in the seeds and the percentage of self-colored ears produced from the various classes of variegated seeds; and (3) the entire absence of variegated ears in the progeny of self-colored and near self seeds.

It seems likely that the difference in percentages of self-colored ears from the several classes of variegated seeds is without significance. Only a single self-colored ear appeared in the progeny of any one class of these seeds. It is perhaps, however, significant that no regular increase in self-colored ears appears as we pass from the very light variegated seeds with very little color, to the dark-crown variegated seeds which have considerable color, particularly at the crown. The possible significance of this fact will be considered later.

The percentages of self-colored ears in the plants grown from self or near self seeds, from more than half self seeds, from less than half self seeds, from variegated seeds (all classes of the latter being lumped together), and from colorless seeds, approximately 51.1, 27.5, 6.9, 0.3 and 0, respectively, are similar to the percentages calculated from results previously reported (EMERSON 1914). The combined results, including all data now available, are brought together in table 2.

TABLE I

Progenies of different classes of maize seeds from seventy-five heterozygous variegated ears cross-pollinated by colorless maize.

Seeds planted	Progenies						
	Number of plants			Total	Percentages		
	Self-colored ears	Variegated ears	Colorless ears		Self-colored ears	Variegated ears	Colorless ears
Self and near self.....	23	—	22	45	51.11	—	48.89
More than half self.....	14	5	32	51	27.45	9.81	62.74
Less than half self.....	6	38	43	87	6.90	43.68	49.42
Dark-crown variegated.....	—	91	78	169	—	53.85	46.15
Medium variegated.....	1	159	209	369	.27	43.09	56.64
Light variegated.....	1	48	41	90	1.11	53.33	45.56
Very light variegated.....	1	141	125	267	.37	52.81	46.82
Colorless	—	31	31	62	—	50.00	50.00
Total	559	581	1140	1140	49.04		50.96

TABLE 2
Progenies of different classes of maize seeds from heterozygous variegated ears cross-pollinated by colorless maize.

Seeds planted	Progenies					
	Number of plants			Percentages		
	Self-colored ears	Variegated ears	Colorless ears	Total	Self-colored ears	Colorless ears
Self and near self.....	37	—	36	73	50.68	49.32
More than half self.....	18	7	34	59	30.51	57.63
Less than half self.....	9	43	52	104	8.65	50.00
Variegated	10	704	734	1468	.68	51.36
Colorless	—	58	51	109	—	46.79
Total	886		927	1813	48.87	51.13

That the percentage of self-colored ears in the progeny is roughly proportional to the amount of self color in the seeds planted is evident. Since the parent ears were heterozygous for variegated pericarp, the V factor was simplex. On the basis of the hypothesis advanced in my former paper, if this single V factor is changed to an S factor early enough so that the whole pericarp is self-colored, the gamete concerned is assumed always to arise from a modified cell containing S instead of V . Since V , from which S came, was simplex, S will also be simplex. Half the gametes formed in connection with self-colored seeds will, therefore, carry S and half will carry a factor for colorless pericarp, so that half the plants resulting from such self-colored seeds should have self-colored ears and half colorless ears. This expectation has been almost exactly realized.

If the seeds that are classed here as more than half self-colored are assumed to average 75 percent self and those classed as less than half self-colored are assumed to average 25 percent self, the percentages of plants with self-colored ears expected from them are 37.5 and 12.5 respectively. The percentages actually observed were 30.51 and 8.65 respectively, a sufficiently close approximation to expectation when allowance is made for the fact that the seeds planted may not have averaged 75 percent and 25 percent as assumed.

Perhaps the most striking feature of these results is the total lack of variegated ears in the progeny of self and near self seeds. This is in exact accord with expectation, since if a simplex V mutates to an S , V could be present in no gamete associated with a self-colored seed. The number of plants from self-colored seeds in table 2 is small, to be sure, totaling only 73. It is permissible, however, to add to this number the records of HARTLEY (1902), of EAST and HAYES (1911, pp. 106-107) and of my own open-pollinated cultures (EMERSON 1914), since the parent ears in all these cases were obviously heterozygous for variegated pericarp and were presumably pollinated from colorless plants. Combining all these lots, we have from self and near self seeds 186 plants with self-colored ears, 177 with colorless ears, and not a single plant with variegated ears.

A noteworthy point in connection with this result is that many, doubtless most, of the seeds planted were not wholly self-colored but were what are here called near self, that is, they had a small colorless or nearly colorless spot at the crown. It will be recalled that the dark-crown variegated seeds (table 1) produced no self-colored ears though they are characterized by dark colored crowns corresponding almost exactly

to the light crowns of the near self seeds. It would appear, therefore, that there is no connection between the color at the crown of the seed and the production of self-colored ears in the next generation. ↓

We have now to consider the behavior of variously colored seeds from homozygous variegated parent ears. All these ears were cross-pollinated by colorless maize just as were the heterozygous ears considered heretofore. Seeds of various color types were selected from 80 homozygous variegated ears and a total of 1972 plants grown from them. The results are recorded in table 3.

TABLE 3

Progenies of different classes of maize seeds from eighty homozygous variegated ears cross-pollinated by colorless maize.

Seeds planted	Progenies				
	Number of plants			Percentages	
	Self-colored ears	Variegated ears	Total	Self-colored ears	Variegated ears
Self and near self.....	71	72	143	49.65	50.35
More than half self....	43	67	110	39.09	60.91
Less than half self.....	16	150	166	9.64	90.36
Dark-crown variegated..	1	528	529	.19	99.81
Medium variegated.....	2	607	609	.33	99.67
Light variegated.....	2	125	127	1.57	98.43
Very light variegated...	1	269	270	.37	99.63
Colorless	—	18	18	—	100.00

Here, just as with the heterozygous variegated parent ears, the several classes of variegated seeds showed no regular difference as to the percentage of self-colored ears produced. The considerable amount of color at the crown of dark-crown variegated seeds, as noted before, has no apparent relation to the production of self-colored ears in the progeny.

The percentages of plants with self-colored ears from the five classes of seeds—self or near self, more than half self, less than half self, variegated (all classes together), and colorless—are not far different from the percentages found in case of heterozygous parent ears, as can be seen from the following comparison (table 4).

The important point here is that, when the variegation factor is duplex, the percentage of self-colored ears in the offspring is not greater than when that factor is simplex. This indicates that ordinarily only one

TABLE 4

Self-colored ears in progenies of different classes of seeds from homozygous and heterozygous variegated ears cross-pollinated by colorless maize.

Seeds planted	Percentage of self-colored ears	
	Homozygous parents	Heterozygous parents
Self and near self.....	49.65	50.68
More than half self.....	39.09	30.51
Less than half self.....	9.64	8.65
Variegated39	.68
Colorless	0	0

of the duplex factors of a sporophytic cell mutates. That is, VV becomes VS not SS . Both V factors may at times change to S factors, but such is not the case frequently enough to affect materially the percentage of self-colored ears and no test other than percentage differences is available. This question has been discussed elsewhere (EMERSON 1913).

Since only one of the duplex V factors ordinarily changes to an S factor in any one sporophytic cell, and if one V factor mutates as readily as the other, it follows that on the average about twice as many self-colored seeds should be found on homozygous as on heterozygous variegated ears. The same difference should be noted in the progenies of non-colored maize when cross-pollinated by homozygous and heterozygous variegated-eared plants. Attention is being given to this matter at the present time.

As noted earlier in this discussion, some of the ears classed above as homozygous were in reality the result of a cross of two distinct strains of variegated maize, one medium variegated and the other very light variegated. While there is some variation in both of these strains, particularly in the medium variegated one, some ears having more color than others, there is no overlapping between them. Ears of the very light variegated strain often appear colorless until examined somewhat closely. A single cross between this strain and a self-colored strain gave sharp segregation in F_2 into self-colored and very light variegated ears with none medium variegated. Numerous crosses of medium variegated with self-colored strains have likewise thrown self-colored and medium variegated offspring with no very light variegated ears. Self color is dominant to both types of variegation. Finally, crosses between the two

variegated strains have shown medium variegation to be dominant to very light variegation in F_1 and have resulted in simple Mendelian segregation in F_2 .

Both medium variegated and very light variegated strains have occasional seeds that are self-colored, near self, half self, etc., though this is much less common in the very light variegated strain than in the medium variegated one. The F_1 medium variegated ears from the cross of the two strains also, of course, have some such seeds. A study of the progeny of the several classes of seeds from thirty of these F_1 variegated ears, a total of 747 plants, has given important results of a kind not heretofore reported. They are brought together in table 5.

The important features of these records are: (1) The percentage of plants with very light variegated ears was not greater when the seeds planted were very light variegated than when they were medium and dark-crown variegated. From all classes of variegated seeds together, approximately 49 percent of the offspring were medium variegated and 51 percent very light variegated, where 50 percent of each was to have been expected. (2) The percentage of self-colored ears was roughly proportional to the amount of self color in the seeds planted. The deficiency of self-colored ears below the expected 50 percent from near self seeds is probably without significance, being due most likely to the small numbers involved. (3) The percentage of medium variegated ears decreased as the percentage of self-colored ones increased. Evidently, the self-colored ears were produced at the expense of medium variegated ears and not at the expense of very light variegated ones.

The significance of this is that in these F_1 plants the factor for medium variegation mutates much more frequently than the factor for very light variegation,— V_mV_l ordinarily becomes SV_l rather than V_mS . This is to be expected from the fact that self-colored and near self seeds occur much less frequently on very light variegated ears than on medium variegated ones. Whether V_mV_l ever becomes V_mS cannot now be said for no evidence is available. This probably does occur, however, for there is abundant evidence that V_lV_l does occasionally, though rarely, become V_lS .

CHANGES IN TYPE OF VARIEGATION

Both medium and very light variegated ears of maize are quite as likely to exhibit pronounced sporophytic variations to dark-crown variegation as to self color. The dark crown spots of these seeds make a "freak patch," or even a single seed, to stand out from the normally

TABLE 5
Progenies of different classes of seeds from thirty F_1 variegated ears of a cross between medium variegated and very light variegated strains, pollinated by colorless maize.

Seeds planted	Progenies					Percentages		
	Number of plants					ears		
	Self-colored ears	Medium variegated ears	Very light variegated ears	Total	Self-colored ears	Medium variegated ears	Very light variegated ears	
Self and near self.....	16	—	27	43	37.21	—	62.79	
More than half self.....	16	7	31	54	29.63	12.96	57.41	
Less than half self.....	8	25	35	68	11.76	36.77	51.47	
Dark-crown variegated	—	92	108	200	—	46.00	54.00	
Medium variegated	—	102	104	206	—	49.51	50.49	
Very light variegated	—	91	85	176	—	51.70	48.30	
Total	40	317	390	747	5.35	42.44	52.21	

colored seeds of the same ear almost as strikingly as does a patch of near self seeds. The fact that dark-crown variegated seeds are almost if not quite universally underlaid by a self-colored cob patch corresponding accurately in outline to the patch of seeds with dark crowns adds not a little to the distinctiveness of this sporophytic variation (figure 3 A, B). In my first paper (EMERSON 1914), it was noted that there was then no evidence of the inheritance of this variation. The same statement might suffice even at present, but the evidence against such inheritance is now so strong that it seems important to present it here, if for no other reason than to emphasize a surprising difference between two almost equally striking sporophytic variations that often occur on the same ear.

Occasionally an ear is found to be divided sharply into two parts, one consisting of seeds that show the ordinary medium-variegation pattern and the other of seeds that are light variegated. Such variations have been much less common in my material than the occurrence of dark-crown variegated and near self seeds. In addition to these very distinct variations, many medium variegated ears have some grains showing all gradations from medium to light or very light variegation.

Of all the instances of sporophytic change in type of variegation that I have investigated, only a few afford any indication of having reached the germ plasm. All these occurred in a single lot of maize. A medium variegated ear with variegated cob, cross-pollinated by a strain of maize with colorless grains and self-colored cobs, produced both medium variegated and very light variegated offspring, all, of course, with self-colored cobs. The parent was, therefore, heterozygous for the two types of variegation. Since it was pollinated by colorless maize, both types of offspring must have been heterozygous, the one for medium variegation and the other for very light variegation. If V_m and V_l are allelomorphic, as there is every reason to believe, no ear could have contained both of these factors. An ear of this lot with medium variegated grains and red cob was self-pollinated and next generation gave colorless ears with self-colored cobs, medium variegated ears with self-colored cobs, and medium variegated ears with variegated cobs, in a ratio approximating 1 : 2 : 1, as was expected of it. No light variegated ears were noted and, of course, none were expected. Since self color of cob is allelomorphic to variegated color of grains, the ears with self-colored cobs were obviously heterozygous for pericarp color as well as for cob color and those with variegated cobs were homozygous. The latter may, therefore, be designated as V_mV_m . Three of these homozygous medium

variegated ears had more or less distinct "freak" patches of rather light variegated seeds. The two classes of seeds from these three ears were planted separately with the following results (table 6).

TABLE 6

Progenies of medium variegated and light variegated seeds of homozygous medium variegated parent ears cross-pollinated by colorless maize.

Seeds planted	Number of plants		
	Medium variegated ears	Light variegated ears	Very light variegated ears
Medium variegated	64	12	0
Light variegated	41	10	18

The ears recorded as medium variegated and light variegated respectively were not sharply separable on account of numerous intermediates and should possibly have been classed together. The very light variegated ears, on the other hand, were a fairly uniform lot and were distinctly lighter than the lightest of the ears classed as light variegated. The striking feature of these records is the fact that no very light variegated ears were produced from medium variegated seeds, while from the light variegated seeds of the same parent ears there were 18 plants, about 26 percent of the total number, with very light variegated ears.

Upon the behavior of such very light variegated ears in later generations will depend the answer to the question whether they are true mutations. Until such tests can be made, it is perhaps idle to speculate about the possible manner of their origin. There are two features of the result, however, that deserve comment. We know that the parent ears were $V_m V_m$ and that they were pollinated by colorless maize. If it be assumed that the very light variegated ears arose through a change of V_m to V_l ,—the only assumption that seems at all reasonable,—how can we explain the visible somatic modification, and how account for the fact that only about 26 percent rather than 50 percent of the ears from the light colored seeds were very light variegated?

If $V_m V_m$ change to $V_l V_l$, the seeds should be very light variegated, but in that case 100 percent of the progeny should be very light variegated. If $V_m V_m$ becomes $V_m V_l$, 50 percent of the offspring should be very light variegated but the parent seeds themselves should not have been affected,

since medium variegation has been found to be dominant to very light variegation. As a matter of fact my descriptions, made, of course, the year before these results were obtained, indicate that the parent seeds were not what I have termed very light variegated, but were merely sufficiently lighter than the medium variegated seeds of the same ears to be readily detected when found in solid patches on those ears. Perhaps medium variegation is not always completely dominant over very light variegation. This, however, since I have not noted partial dominance in actual crosses between these types, is so obviously an attempt to make the facts fit the hypothesis that the matter had best be dismissed with the mere statement that the record presented here is the only evidence, slight as it is, that a sporophytic change in type of variegation of maize pericarp is ever of the nature of a true mutation.

From various other ears both homozygous and heterozygous for medium variegated pericarp, light and very light variegated seeds scattered over the ears have been selected and have given no evidence of the inheritance of the type of variegation shown by them. The available data are given in table 7. The records are grouped so that parent ears of like nature, homozygotes or heterozygotes, are classed together.

From many of the same parent ears employed for the comparison given in table 7 and from some others, ninety-one in all, dark-crown variegated seeds were selected for planting in comparison with medium variegated seeds of the same ears. The data obtained from these tests are given in table 8.

It is obvious that, so far as the available data go, they give no indication that dark-crown variegation occurring as a sporophytic variation is ever inherited. This behavior is noteworthy in contrast to the definite inheritance of self or near self color when it occurs as a sporophytic variation in variegated maize—the more particularly so because the visible change is quite as definite and almost as striking in the one case as in the other. The cause of this difference is reserved for discussion later in this paper.

The possible inheritance of self color of the cob, which occurs as a sporophytic variation, so far as I have observed, universally associated with dark-crown variegated seeds on otherwise variegated cobs, is of even more interest than the inheritance of variations in pericarp color. Dark-crown variegation of maize seeds does not, so far as I am aware, exist except as a sporophytic variation, while self color of the cob is always associated with the more common self colors of the pericarp,

TABLE 7

Progenies of light variegated and of medium variegated seeds from seventy-two homozygous and heterozygous variegated ears.

Seeds planted	Progenies						
	Number of plants						Percentage
	Medium variegated ears	Light variegated ears	Very light variegated ears	Colorless ears	Total	Light variegated ears	
Twenty-one ears— Medium variegated....	118	7	—	—	125	5.60	—
Light to very light variegated	111	6	—	—	117	5.13	—
Twenty-four ears— Medium variegated....	82	8	—	98	188	4.26	—
Light to very light variegated	27	3	—	24	54	5.56	—
Twenty-seven ears— Medium variegated....	122	8	167	—	297	2.70	56.23
Light to very light variegated	44	4	49	—	97	4.12	50.52

TABLE 8
Progenies of dark-crown variegated and of medium variegated seeds from ninety-one homozygous and heterozygous variegated ears.

Seeds planted	Progenies						Percentage		
	Number of plants						Dark-crown variegated ears	Light variegated ears	Very light variegated ears
	Dark-crown variegated ears	Medium variegated ears	Light variegated ears	Very light variegated ears	Colorless ears	Total			
Twenty-seven ears— Medium variegated....	—	243	9	—	—	252	—	3.57	—
Dark-crown variegated	—	200	1	—	1	202	—	.50	—
Thirty-seven ears— Medium variegated....	—	76	9	—	114	199	—	4.52	—
Dark-crown variegated	—	64	4	2	60	130	—	3.08	1.54
Twenty-seven ears— Medium variegated....	1	134	9	141	—	285	.35	3.16	49.47
Dark-crown variegated	—	70	3	91	—	164	—	1.83	55.49

dark red and dark brown, and is frequently found in strains with colorless pericarp.

Unfortunately, the occurrence of self-colored cobs in the progeny of dark-crown variegated seeds cannot in these studies be taken as an indication of the inheritance of a sporophytic variation in cob color, for the reason that a considerable number of the plants used as pollinizers, though colorless as regards pericarp, had self-colored cobs. A part of the progeny of all seed classes was, therefore, expected to have self-colored cobs, so that the only criterion of the inheritance of sporophytic variation to self color in cobs is the relative percentages of plants with self-colored cobs in the progenies of dark-crown variegated and of medium variegated seeds.

Of the 1057 plants with variegated ears listed in table 8, 435 came from dark-crown seeds all of which were associated definitely with self-colored patches of the otherwise variegated cobs to which they were attached, while 622 grew from medium variegated seeds associated with variegated cob patches of the same ears. All these plants with variegated ears had variegated cobs except 60 of those from dark-crown seeds and 88 of those from medium variegated seeds. The percentages of plants with self-colored cobs were, therefore, about 13.8 for the progeny of dark-crown seeds and about 14.2 for the progeny of medium variegated seeds. Of 1486 plants grown from seed of the plants with colorless pericarp and colorless cobs used as pollinizers, 208, or almost exactly 14 percent, had self-colored cobs. There is certainly nothing in these results to indicate that a sporophytic variation from variegation to self color of the cob is inherited.

REVERSE MUTATION—SELF COLOR TO VARIEGATION

In certain cultures of maize there have been noted ears that are self-colored except for a single variegated grain or a grain that is half variegated and half self, one-third variegated and two-thirds self, etc. Frequently, two or three and in a few cases as many as five such grains have been found on a single otherwise wholly self-colored ear. In the records presented earlier in this paper all such ears have been listed as self-colored, and I think rightly so, just as ears that were variegated throughout except for a few self-colored seeds have been listed as variegated. In short, I regard the occurrence of these variegated seeds on self-colored ears as due to sporophytic mutations from self color to variegation. I must admit, however, that there is at present very little direct evidence as to the real nature of these variegated seeds.

Few such variegated seeds have been tested and most of these have not been wholly desirable material for the tests. The seeds tested were found mainly on ears that were heterozygous for self-colored and variegated pericarp, SV . Even the self-colored seeds of these ears should throw 25 percent or 50 percent variegated ears the next generation, the actual percent depending, of course, upon whether the parent ear was self-pollinated or crossed by colorless maize. If the S factor of such an ear change to V the result would be to produce homozygous VV tissue. Any seed in the modified part of the ear would be variegated. But collectively such seeds would produce only 50 percent of variegated offspring if self-pollinated, because half the pollen would carry dominant S , and 100 percent variegated if crossed by colorless maize. The only criterion of the assumed mutation is, therefore, a difference in percentages of variegated offspring from the self-colored and variegated seeds of the same ear. This would be fairly conclusive if larger numbers could be dealt with, but since the numbers that can be grown are small owing to the rarity of such variegated seeds, the results are not satisfactory.

Self-colored ears that are heterozygous for self-colored and colorless pericarp afford satisfactory material but as yet I have been unable to take full advantage of it. Half the gametes of such a plant ordinarily carry the S factor and the other half carry a factor for colorless pericarp. If then S become V in connection with variegated grains and if the ear were cross-pollinated by colorless maize, the variegated seeds should throw 50 percent variegated and 50 percent colorless offspring while the self-colored seeds should throw 50 percent self-colored and 50 percent colorless offspring. The failure of self-colored seeds to produce variegated ears and of variegated seeds to produce self-colored ears would furnish definite evidence of a factorial change. Large numbers would not, therefore, be required.

If, on the other hand, this self-colored ear, heterozygous for pericarp color, were self-pollinated, the self-colored seeds would, of course, throw 75 percent self-colored and 25 percent colorless ears, while the variegated seeds of the same parent ear would produce 50 percent self, 25 percent colorless and 25 percent variegated. But here comparison of ratios is not necessary—the mere presence of variegated ears, barring accidental pollination, is evidence of the factorial change from S to V . From a few variegated and partly variegated seeds from self-pollinated parent ears, all the expected classes of ears—self, colorless, and variegated—have been obtained. Only a single variegated ear, however, has been

produced from the few variegated seeds tested. This ear was self-pollinated and threw only variegated and colorless offspring, just as was expected on the basis of the assumed factorial change. But the same result would necessarily have followed if the variegated ear in question had been produced through the action of a stray grain of pollen carrying V on a seed that might otherwise have produced a colorless ear. While the chance is rather small that such a stray grain of pollen might have happened to fertilize one of the very few variegated seeds of the parent ear rather than one of the numerous self-colored seeds, the possibility is not excluded. No adequate evidence, therefore, of a factorial change from S to V is available. It can merely be said that such a change is strongly suggested. The assumption of factorial change is strengthened by the fact that the variegated ears of this lot are more fully colored than those of any other variegated strain in my collection. The few ears observed have more seeds near self, half self, etc., than other strains and more color on the variegated seeds. Moreover, this tendency has persisted to the second generation.

It is of interest to note the fact that in some lots of self-colored maize, which have arisen by sporophytic mutation from variegated strains, no variegated or partially variegated seeds have ever been observed. In other lots, on the contrary, the tendency is very strong to produce a few variegated seeds on the otherwise self-colored ears. In most of these cultures from one-third to two-thirds of the self-colored ears have a few variegated grains. It seems particularly noteworthy that the only cultures to show this apparent reverse mutation trace back to one or the other of two ears of maize obtained some years ago. Some lines of self-colored maize originating from these same two ears have, on the other hand, never shown a tendency to produce variegated seeds.

From all this it seems likely that, if the sporophytic variation here under consideration is a reversal of the common mutation which goes from V to S , there are differences between the S factor of different strains in respect to the frequency with which it may change to a V factor just as there are different sorts of V factors, one of which, V_m , mutates more readily than another, V_l . The possibility, however, that the difference may not be inherent in the S or V factors themselves, but may be due to some interaction of other factors with the S or V factor in certain strains is not precluded.

Another point of no little interest is the fact that up to the present time no variegated seeds have been found on ears known to be homozygous for self color, SS , though they have appeared frequently in re-

lated heterozygous families, in which S was simplex and associated with simplex V or with a factor for colorless pericarp. This, if found to hold when further results have been obtained, will have a bearing upon the question of whether both of the duplex factors ever mutate at the same time (see EMERSON 1913). It has been shown earlier in this paper that as a rule only one of the duplex factors VV mutates, thus giving rise to SV rather than SS . Owing to the dominance of S over V , a mutation of S to V affecting only one of the duplex factors in homozygous self-colored maize, would not be visible as a somatic variation, for VS could not be distinguished from SS .

SUGGESTED EXPLANATION OF THE INHERITANCE OF CERTAIN SPOROPHYTIC VARIATIONS AND THE NON-INHERITANCE OF OTHERS

In this and earlier papers, it has been shown that a sporophytic variation from variegation to near self color of the pericarp of maize is definitely inherited, while quite as striking a variation from light and medium variegation to dark-crown variegation of the pericarp is never inherited. The contrast is particularly noteworthy because the non-inherited dark-crown variegation is apparently always associated with a change in cob color from variegation to self pattern, this change also being non-inherited, while the inherited near self variation of the seed is accompanied by only a slight change in cob color, though the self-colored ears produced by such seeds always have self-colored cobs.

When the difference in behavior was first recognized, it seemed possible that it might be related in some way to the stages in ontogeny at which the sporophytic variations in question arise. It was assumed that the modification to self color takes place previous to the differentiation of the megaspore mother cell and in the direct line of its cell ancestry. On the other hand, the fact that much color develops only near the crown of the seeds of the non-inherited dark-crown variation suggested that this modification might occur late in the development of the pericarp and, therefore, in a line of cell generations collateral to that from which the germ cell arises, rather than in direct line with it. A notable difficulty with any such hypothesis is that a factorial change occurring late in the development of the pericarp could hardly be supposed to influence the color of the underlying cob so that every dark-crown seed would be associated with a self-colored cob spot. Moreover, to account for large patches of near self seeds, it had to be assumed that the factor change might sometimes take place almost simultaneously in the rudiments of every grain so that the grains become self-colored

while the cob remains variegated (EMERSON 1914). The universal appearance of self-colored cobs with self-colored seeds in the progeny of these near self seeds led naturally to subsidiary hypotheses concerning the simultaneous modification of factors for cob and pericarp color (EMERSON 1913).

If further investigation confirms the indications already at hand, all these facts can be harmonized and explained on a simple histological basis, which will render at least some of the hypotheses unnecessary and unwarranted. Microscopic sections of mature seeds made for me by Mr. E. W. LINDSTROM, graduate student in genetics at CORNELL UNIVERSITY, indicate plainly that the outer epidermal layer of cells of the pericarp of near self seeds is without color while the underlying part of the pericarp, except at the crown of the seeds, is largely, if not wholly colored. In contrast to this condition, the dark-crown seeds certainly have color in the outer epidermis of the pericarp and, except at the crown, lack color in much of the underlying part of the pericarp. The sections also show indisputably that there is some deep-lying color even at the sides of these dark-crown grains, but whether this color is confined to epidermal cells has not been determined. According to TRUE (1893), the integuments of the ovule, which are mostly two cells thick and therefore probably mostly epidermal, largely disintegrate as the seed develops, but the thick-walled cells of the inner epidermis of the pericarp remain intact. There is also a possibility that the epidermis of the nucellus may have contributed slightly to the color observed in sections of dark-crown seeds. Wholly self-colored seeds of plants produced from the near self variation apparently have color in both the epidermal and the sub-epidermal cells of the pericarp.

Sections of very young maize ears furnished me by Mr. E. G. ANDERSON, graduate student in genetics at CORNELL UNIVERSITY, show the glumes to have only two layers of cells, except near the base where they are several cells in thickness. From this I infer that even the mature glumes are largely epidermal in origin. If this be true, the dark-crown variation, in which the color is now suspected of being confined to the epidermal layers, would necessarily be associated with self-colored cob spots, while the near self seeds, with presumably no color in epidermal tissue would be associated with glumes that were non-colored, except at their thick bases. The wholly self-colored seeds produced in the next generation by near self seeds should, of course, have self-colored cobs because here there is color in the epidermis as well as in the sub-epidermal cells.

There yet remain to be explained the light crown spot of near self seeds, the exactly corresponding dark crown spot of dark-crown variegated seeds, and the lack of color differentiation at the crown of seeds of self-colored ears produced by near self seeds. While the matter can be settled definitely only by a study of the developing seeds, there are some reasons for the belief that the crowns of maize seeds are largely epidermal in origin. The exact correspondence in pattern between the colored lines converging at the point of attachment of the silk of dark-crown grains and the light spot of near self seeds has been noted repeatedly. So far as I have observed self-colored seeds occurring individually or in small groups within a large "freak" patch of dark-crown seeds and self-colored cob always lack the light crown spot. Likewise, in a large patch of near self seeds with variegated cob, there sometimes occur small patches of self-colored cob and, so far as observed, the seeds of the small patches are wholly self-colored, lacking the light crown spots.

All of these peculiarities of coloration of seeds and cobs are thus readily harmonized, if it turns out on further study that the color of the dark-crown variation is limited to epidermal tissue and the color of the near self variation to sub-epidermal tissue. And, more important still, no other explanation of the non-inheritance of the one type and the inheritance of the other is needed. Sporophytic changes occurring in epidermal cells can, of course, have no influence upon the germ cells which arise from sub-epidermal tissue. Modifications of genetic factors in epidermal cells are doubtless not fundamentally different from such changes in sub-epidermal cells, but if the inheritance of a variation is to remain the criterion of mutation, mere epidermal variations must be regarded at most as nothing more than potential mutations.

In various papers (EMERSON 1911, 1913, 1914), it has been assumed that factors for colors or color patterns of the pericarp are distinct from similar factors of the cob glumes and that these glume and pericarp factors are closely linked. These assumptions were made to account for such observations as the following. When a race having color in both glumes and pericarp is crossed with one lacking color in these parts, no new combinations of glume and pericarp color are produced. When a race having self-colored cob glumes and colorless pericarp is crossed with one having colored pericarp and colorless or nearly colorless glumes, F_1 has color in both glumes and pericarp, but produces no gametes bearing factors for this combination of colors, so that in F_2 there appear only the parental and F_1 combinations, never colorless glumes with colorless pericarp. It was natural to suppose that also in case of variegated peri-

carp and cob glumes separate factors were concerned, namely, \bar{V}_p and V_o . To account for the appearance of self-colored cobs with self-colored seeds in the next generation from near self seeds occurring as somatic variations on otherwise variegated ears, it seemed necessary to assume a simultaneous modification of V_p and V_o to S_p and S_o . And this occurrence it was suggested might be due to the close association of V_p and V_o in the chromosomes.

The histological explanation suggested above, of the inheritance of certain, and the non-inheritance of other, sporophytic variations, if found to be correct, will make it seem more likely that the self color and variegation factors responsible for the color patterns of the pericarp are the identical factors concerned with the same color patterns in the glumes. Attention has already been called by MORGAN *et al.* (1915) to the possibility that I have been dealing with cases of multiple allelomorphs rather than with closely linked factors. In the light of the present study MORGAN's view seems the more reasonable one.

If the explanation here suggested for the inheritance of certain sporophytic variations in maize and the non-inheritance of others is found to be the true one, it will be of interest to investigate similar situations in other plants. It will be remembered that DE VRIES (1905, pp. 309-328) reported the inheritance of a sporophytic change from variegated to self red flower color in *Antirrhinum*, while CORRENS (1910) described a similar variation in *Mirabilis* flowers, that is not inherited. I have previously suggested (EMERSON 1914) that these cases may be similar to the inherited and non-inherited sporophytic variations in maize. At present there is nothing more than this resemblance in behavior to suggest a similar explanation, but it is proposed to investigate the situation in these and other variegated flowers.

RELATION OF VARIEGATION TO UNIT-FACTOR CONSTANCY

If the results here recorded have been correctly interpreted, they have an important bearing upon the question of unit-factor constancy. Self-color arises from variegation and is then inherited as a simple allelomorph to variegation. It follows, therefore, that a unit factor concerned in the development of variegated pericarp is occasionally changed to a factor concerned in the development of self color. Moreover, the same change—or a change that produces the same end result—occurs repeatedly. There is some evidence also that a factor for self color thus produced may, by a reverse mutation, become again a factor for variegation.

* The variegation and self-color factors belong to a series of not less than nine or ten multiple allelomorphs which include self red and self orange, white-capped red, basal red, and colorless pericarp, associated with either self red or white cobs, and at least three types of variegated pericarp associated with similarly variegated cobs. The fact that such a series of multiple allelomorphs exists is evidence that a fundamental factor concerned in the development of pericarp and cob colors and color patterns has at one time or another mutated in diverse ways. That these several factors are distinct, not merely with respect to the end results which they help to produce as exhibited in types of coloration of mature ears, but also as regards the relative frequency with which they are now mutating, is obvious to anyone who has worked with ear colors of maize. Only two instances of sporophytic changes from self red to white—or perhaps they were from white to red—have been observed by me. Both of these variations were accompanied by modifications of the fundamental color factor concerned (EMERSON 1914). I have also found two ears with both self red and self orange, or brownish orange, seeds in separate patches. There is some scarcely conclusive evidence that in these cases also factorial modifications were responsible for the somatic variations observed. In no other instances, not involving variegation, have such changes been noted. When it is remembered that large numbers of individuals of these types have been studied in pure strains and in crosses, the rarity of such factorial changes becomes evident.

There is some evidence that a self-color factor, that has arisen by mutation from a variegation factor, may, by a reverse mutation, become a variegation factor. The change is comparatively infrequent, not more than five variegated seeds ever having been found on any one otherwise self-colored ear. But it occurs with considerable regularity, for from one third to two thirds of the ears of some heterozygous or partly heterozygous lots have one or more variegated seeds. In some strains of self-colored maize that have arisen by mutation from variegated strains, no tendency to a reverse mutation has been observed. It seems possible, therefore, that there exist distinct self-color factors which produce identical end results—self color—and which differ in no way except in relative frequency of mutation.

Certainly there exist two, and probably three, distinctly different types of variegated pericarp. The most obvious difference between them is in the amount of red (or brown) color produced. But the fundamental difference is probably only a matter of relative frequency of

factorial change. One type is very light variegated, i. e., has little red (or brown) color—few more or less fully self-colored seeds and few even that are prominently striped with color—because the factor concerned changes to a factor for self color comparatively rarely. Medium variegated types have more self-colored seeds and more seeds with prominent stripes of color because in them the factorial change occurs more frequently. In very dark variegated maize (a type little studied as yet) the same change takes place with still greater frequency.

In all types of variegated pericarp, ears with all or nearly all seeds self-colored or near self are less common than ears with small patches of near self seeds. Ears of the latter sort are less common than those with scattered near self seeds. Near self seeds are less commonly seen than half self and the latter less commonly than seeds with broad self-colored stripes. Most common of all are narrow streaks of color. Practically all seeds of medium variegated ears have numerous streaks of that kind. Even the lightest variegated ears have some seeds so marked. All this, I am inclined to believe—although perhaps there is not sufficient evidence to substantiate it—is because the factorial change occurs with increasing frequency in the later stages of ontogeny. If this is true, the several types of variegated pericarp differ in frequency of factorial change by virtue of the fact that the change begins earlier in some types than in others. On this basis colorless seeds of very light variegated ears might be regarded as the extreme of delayed factorial change, for such seeds produce variegated ears rather than colorless ones in later generations.

According to this interpretation, then, there are, in this somewhat remarkable series of multiple allelomorphs, many degrees of factorial constancy. On the one extreme are self-colored and colorless races, both as constant probably as most Mendelian characters. Next to these are the self-colored types that exhibit from one to four or five variegated or partially variegated seeds on perhaps a majority of the heterozygous ears. Then comes the very light variegated type in which a factorial change to self color comparatively rarely occurs at a sufficiently early stage in ontogeny to affect the germ cells but somewhat more frequently at later stages. At the other extreme is a little known type of very dark variegation in which the factorial change occurs so frequently that all ears, so far as observed, have numerous self-colored or near self seeds. Medium variegated races—probably of more than one type—occupy an intermediate place in the series.

There can be no question that at least the more distinct types of

variegated pericarp are inherited in a simple Mendelian way. They segregate out sharply and apparently without contamination. While the factorial changes described are doubtless non-Mendelian, they are in no sense anti-Mendelian. Genetic modifications are not the concern of Mendelism but of mutation. The essential feature of Mendelism is the segregation of unit factors without their contamination. There is a tendency on the part of some to add as another essential the absolute constancy of unit factors. Doubtless most geneticists who have dealt at first hand with Mendelian phenomena regard unit factors as relatively stable. Few presumably, who have studied pedigree cultures extensively, would hesitate, however, to admit the possibility of an occasional rare mutation. If any unit factor may possibly be modified once, may not others change many times? Much recent work, connecting genetical behavior with the cytological phenomena of reproduction, affords convincing evidence that unit factors are, or have their basis in, material substances. Nothing is better known than that specific, even though closely related, organic compounds differ remarkably in their stability. It seems reasonable, therefore, that specific unit factors might differ widely in constancy. But, whether reasonable or not, they appear in fact so to differ.

Perhaps it is too early to venture further in what may prove to be only fanciful speculation. Whether or not, however, the interpretation here suggested is finally accepted, it will best serve its purpose as a tentative hypothesis if it is boldly followed in whatever way it seems to point. With this as justification, then, it is suggested that some of the divergent results of selection within pure lines, or what pass for pure lines, and in clonal populations may find a rational explanation in accordance with the hypothesis developed in this paper. There seems abundant evidence that selection involving several variable characters within pure lines of the common cereals, for instance, has no effect. On the other hand, unpublished results obtained by WEBBER and MYERS leave little room for doubt that selection is often times effective within tuber-lines of the common potato. It does not seem unreasonable to expect many gradations from organisms, in which on the one hand, particular characters respond somewhat readily to pure-line selection, to organisms with which, on the other hand, it will be impossible to demonstrate any such effect.

In view of the foregoing suggestions and in order that there may be no misunderstanding of my position, it may be well to add that I see no reason for abandoning the pure-line concept which has played so

important a part in the clarification of our ideas of inheritance. While we shall have to recognize that it has limitations, there is little in this study to indicate even a lessening of its importance. Even though factorial modification occurs frequently, it can have little influence upon the trend of evolution, if, as in variegated pericarp of maize, it is merely the same modification occurring again and again, and that modification being subject to occasional reversal. Much less is there anything either in the facts here presented or in the speculations concerning them to justify positive assertions of inconstancy of unit factors when the material employed is of questionable purity or when it has not been subjected to careful factorial analysis.

SUMMARY

Distinct variations in variegated ears of maize are described. Results previously reported have been confirmed with more favorable material and new phases of the problem have been investigated. The seed ears used in the later studies have all been pollinated by colorless strains to avoid difficulties arising from the uncertainty of the purity of the pollen of variegated races. Self-colored, partly self-colored, variously variegated and colorless seeds from variegated parent ears, thus pollinated, have given progenies containing a percentage of self-colored ears roughly proportional to the amount of self color in the seeds planted, the maximum being approximately 50 percent from self-colored and near self seeds and the minimum none from colorless seeds. This has been equally true whether the parent ears have been homozygous or heterozygous for pericarp color. In the latter case, the self-colored ears have always occurred at the expense of variegated ears, never at the expense of colorless ones. Medium variegation has been found to be a simple Mendelian dominant to very light variegation. Self-colored ears appearing in the progeny of F_1 ears of this cross have occurred at the expense of medium variegated ears rather than in the place of very light variegated ones. These facts are held to indicate that a genetical factor for variegation mutates to a factor for self color, that only one of the duplex factors ordinarily so mutates, and that the factor for medium variegation mutates much more frequently than that for very light variegation.

Some evidence has been found to indicate the inheritance of a light type of variegation arising as a sporophytic variation on medium variegated ears, but the matter has not been fully investigated. Sufficient evidence has been obtained to warrant the statement that a sporophytic change in type of variegation, resulting in seeds with strongly colored

crown spots associated with self-colored cob glumes, is not inherited as regards either pericarp or glume color.

In a number of cultures of self-colored maize all descended from two presumably unrelated variegated ears, from one to five wholly or partly variegated seeds per ear have occurred on about two thirds of the otherwise fully self-colored ears. Other related and unrelated cultures have not exhibited such exceptional seeds. No variegated seed has, so far as known, ever occurred on a homozygous self-colored ear. A single test has indicated the inheritance of these presumably reverse mutations from self color to variegation, but the question requires further study.

A preliminary histological examination of the developing maize ovary and glumes and of the mature seed has suggested a possible explanation for the peculiarities of coloration of distinct somatic variations and for the inheritance of some of them and non-inheritance of others. The change from variegated to near self seeds associated with little change in color of the glumes is thought to occur only in sub-epidermal cells and for this reason to stand a chance of being inherited, while the change from variegated to dark-crown variegated seeds accompanied by self-colored glumes is believed to be limited to the epidermal layers and hence to be incapable of inheritance.

It is thought that these results favor the idea that single allelomorphic factors, rather than two or more closely linked factors, are responsible for the color pattern of both glumes and pericarp.

The phenomena studied are held to have an important bearing on the question of unit-factor constancy. The existence of the series of at least nine or ten multiple allelomorphs to which variegation belongs, indicates that a factor for pericarp color has mutated several times. Some of the factors of this series have not been observed to mutate, while others have mutated rarely and still others many times. In fact, the principal difference between certain of the factors is thought to lie in their relative frequencies of mutation. It is suggested that data such as is here presented may help to explain the somewhat diverse results of selection experiments within pure lines, clonal lines, and the like.

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THE CORRELATION BETWEEN BODY PIGMENTATION AND EGG PRODUCTION IN THE DOMESTIC FOWL

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INTRODUCTORY REMARKS

Many poultry breeders have criteria by which they feel able to distinguish the laying from the non-laying birds in their flocks at any time without recourse to trap-nesting.¹

It is perhaps not surprising that with the introduction into agricultural investigations of the exact methods of laboratory experimentation these indirect and scientifically untested criteria should receive but little credence or attention.

Nevertheless it must be admitted that in extended and deep-rooted popular belief there is frequently a minimum of substance as well as a maximum of superstition. We therefore decided to test various popular beliefs against the facts of actual controlled experiments, with a view to

¹ KENT (1916) has recently outlined the criteria employed.

eliminating the mass of superstition and differentiating the kernel of truth if existent.

Such a course seemed to have a two-fold justification.

First, it is perhaps self evident that for many practical breeders trap-nesting is an unattainable ideal. Any method which makes possible the selection of the heaviest layers without the expense of trap-nesting should—providing selection itself is worth while—be of practical value.

Second, egg production in the domestic fowl is a remarkable example of the chemical efficiency of an organism. During the year the 150-egg bird stores in her eggs an amount of fatty and nitrogenous substances which in comparison with her body weight is relatively enormous. It would be highly remarkable if these processes could be carried on without affecting, and perhaps profoundly, the visible somatic features of the organism. If this be true, a study of the correlation between the extent of reproductive activity and somatic characters may have its value from the purely physiological side.

Early in these studies two of us (BLAKESLEE and WARNER, 1915 a, b, BLAKESLEE 1915, WARNER 1916) showed that in certain breeds of poultry, such as Leghorns and the so-called American breeds, including Plymouth Rocks, Wyandottes and Rhode Island Reds, there is in fact a close connection between the amount of yellow pigment to be seen in a bird and her previous laying activity.

Since these observations were published, various comments, criticisms, notes of earlier fragmentary observations, and preliminary notes on work in progress elsewhere have appeared, chiefly in the poultry journals. We shall not, we hope, be considered unfair to other writers if in the present technical treatment of the subject we omit all reference to discussions unaccompanied by quantitative data.

It is our purpose in this place to analyze more minutely, by means of the modern biometric formulae, the data upon which the former conclusions were based and other supplementary series.

In doing this we shall not attempt a comprehensive investigation of all the problems presented by the series of data at our disposal, but shall limit ourselves as strictly as possible to one specific problem, that of the relationship between body pigmentation and egg production. In doing this we are also restricting ourselves to one measure only of pigmentation—the percentage of yellow occurring in the ear lobe of White Leghorns as determined by the color top. This measure is selected because it is probably the most accurate of those available and the most suitable for quantitative expression.

It is, therefore, best fitted for a purely physiological study. The results obtained with this character are substantiated by the results of observations on pigmentation of leg, beak and vent, which will be discussed in detail in a forthcoming bulletin of the STORRS AGRICULTURAL EXPERIMENT STATION.

MEASUREMENTS TAKEN

The amount of yellow in the ear lobe can be conveniently measured quantitatively by means of the Milton Bradley color top. In matching ear lobes against the blend produced by the spinning disk, only yellow and white sectors were used. The matching is not perfect, especially in the lower grades, since a certain amount of blue is often present. The amount of yellow has, however, probably been more accurately measured than if the other color components had been considered. Under proper illumination, it appears possible for an observer to repeat observations with a divergence of not over 5 percent.² In analyzing the results statistically, we have recorded in classes of 5 percent range.

Pigmentation determinations were made October 19-21, 1914 and October 17-18, 1915.

The egg records were taken as a part of the regular routine of the egg laying contest. Such details as are essential concerning this feature of the work will be given below.

ACCURACY OF DATA AND SOURCES OF ERROR

Our data were drawn exclusively from the egg laying competitions conducted for the past four years at Storrs, Conn. The method of procedure in these competitions has been described elsewhere (KIRKPATRICK and CARD 1915).

Pullets enter the competition November 1 and remain for one year. They are housed in pens of 10 birds each, are fed the same ration, and so far as possible are treated exactly alike.³ The influence of environmental factors can therefore be disregarded.

² Tests in the use of the top indicate that some observers have a constant tendency to read higher or lower than others, but that an individual observer tends to estimate consistently. Accordingly, all the color determinations upon which constants are based were taken by the same observer (BLAKESLEE).

³ In 1913-'14 four pens, and in 1914-'15 one pen, belonging to the EXPERIMENT STATION, had sour milk substituted for certain ingredients in the normal ration, but since they showed no apparent difference in color that could be attributed to the change in the feed, they are included in the tabulations.

That the use of such data for physiological studies will be criticized by some we have little doubt. Such criticisms will fall into three principal categories:

1. That the birds entered in these competitions constitute a relatively heterogeneous group of organisms.

The fact that these birds were submitted by a large and widely scattered series of breeders may not, we think, be considered altogether, if at all, a disadvantage. The variety of origin of the birds makes certain that the results are typical of the breeds as a whole, not characteristic of and determined by some peculiarities of a particular experiment station flock.

A certain disadvantage of the materials may possibly lie in the fact that while all the birds were in their pullet year when placed in the competition the exact hatching date of the different lots and the number of eggs which may have been laid by the individuals before they were placed in competition on November 1 is unknown.

The absence of these data is far less important (if of any significance at all) in the kind of problem with which we are dealing in this paper, than they would be in studies involving the records of the total egg production of the first and second year.

2. That the records of egg laying competitions lack the accuracy demanded by scientific investigation.

This we doubt. Relatively large economic importance attaches to the results of these competitions, and every reasonable precaution has been taken to secure trustworthy results.

3. Finally, the objection may be made that the pigmentation determinations by means of the color top could not be carried out with the degree of accuracy necessary for quantitative work.

This objection is not supported by the results of our experience of the past two years, which has shown that it is possible to repeat determinations with a fair degree of consistency, and that experimental errors in matching colors are not great enough to materially influence results when the experiments are carried out on a large scale.

Any objections on these grounds would be equally pertinent to any physiological studies in which the same technique was necessary. The extent of the experiment presents certain great advantages as compared with the usual experimental studies. The number of birds involved was relatively very large. As a result, errors of observation, if not of a systematic nature, will tend to average out.

The smoothness of our results and the remarkable agreement of the

constants for the two years seems to us the strongest *a posteriori* reason to consider the technical details of the work—both those of the egg laying competition, properly so called, and the measurements of pigmentation—as having been carried out with a relatively high degree of consistency and exactness.

PRESENTATION OF DATA AND BIOMETRIC CONSTANTS

As explained above, we shall in this paper limit ourselves as strictly as possible to a consideration of the problem of the relationship between ear lobe pigmentation and egg production. For this purpose it is necessary to know the frequency distribution and the physical variation constants of the characters dealt with.

Type and variation of characters

The frequency of the different percentages of pigmentation in the two years are shown in tables 5 and 6 below, and graphically on a percentage basis in diagrams 1 and 2.

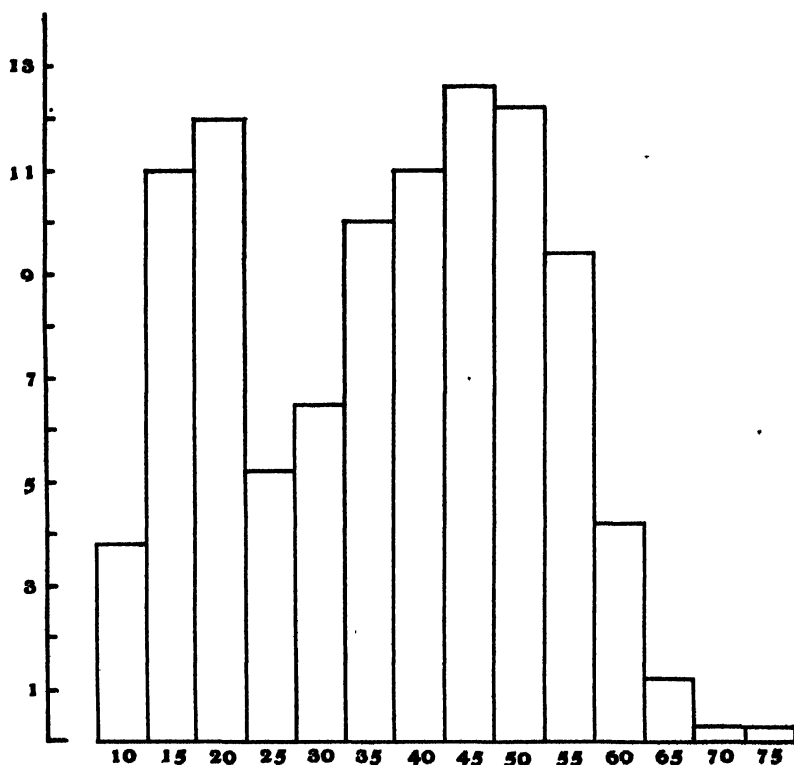


DIAGRAM 1.—Distribution of yellow in five percent classes in ear lobes of White Leghorn hens, 1913-14. Frequencies are reduced to percentages.

These show a highly interesting bimodal condition. The frequency of birds with given percentages of yellow increases from the lowest recorded class, 10 percent, up to 20 percent, beyond which there is a decline in the number of birds observed which reaches its lowest point at 25 or 30 percent. The frequency then rises to a maximum at 45 or 50 percent, after which it again falls. The variation constants in terms of individual percents are as follows:

	Mean	Standard deviation	Coefficient of variation
1913-'14	$36.408 \pm .579$	$15.090 \pm .409$	41.45 ± 1.30
1914-'15	$40.640 \pm .560$	$16.079 \pm .396$	39.56 ± 1.12
Difference	$4.232 \pm .805$	$.989 \pm .569$	1.89 ± 1.72

The difference in the percentage of yellow in the two years is about 5 times as large as its probable error. Such a difference, considered

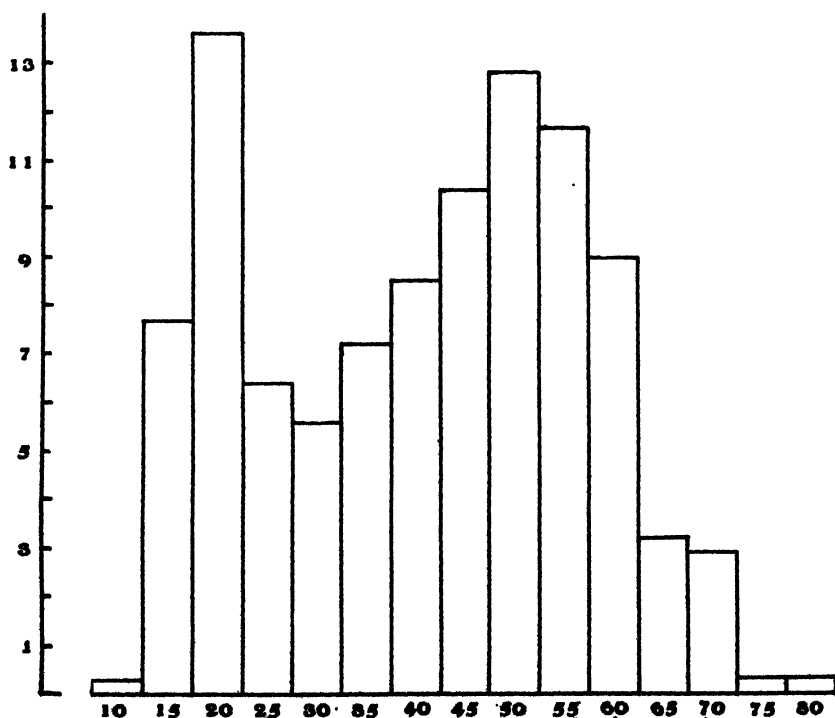


DIAGRAM 2.—Distribution of yellow in five percent classes in ear lobes of White Leghorn hens, 1914-'15. Frequencies are reduced to percentages.

from the purely statistical side, would be looked upon as probably significant. The difference is, however, less than one working unit. When the great difficulties in matching color series under the best conditions are borne in mind, it is not surprising that a difference at least as great as that shown here should be found between the results of two sets of observations separated by an interval of a year.

The variation in the percentage of yellow pigment, measured in the absolute terms of standard deviation or in the relative terms of the coefficient of variation, cannot be said to differ significantly in the two years, when probable errors are taken into consideration.

The variation in number of eggs laid per year is very wide, ranging from 16 to 255 in 1913-'14, and from 0 to 255 in 1914-'15. We give merely the means and variation constants for annual production. These are:

	Mean	Standard deviation	Coefficient of variation
1913-'14	151.63 \pm 1.45	37.85 \pm 1.03	24.96 \pm 0.72
1914-'15	154.48 \pm 1.51	43.22 \pm 1.06	27.98 \pm 0.74
Difference	2.85 \pm 2.09	5.37 \pm 1.47	3.02 \pm 1.03

The mean annual production differs by less than three eggs, or by less than two percent. The birds in the competition in 1914-'15 were perhaps significantly more variable in annual egg production than those studied in 1913-'14.

Notwithstanding the fact that certain differences between the constants for pigmentation and for annual egg production in the two years must be considered statistically significant, the impression which any impartial observer must gain from these constants is that the experiment has been carried out in the two different years with a surprisingly high degree of consistency of results.

For number of eggs laid per month the range is narrow enough that the frequency of birds laying from 0 to 29 eggs, the maximum observed number, may be given for each month individually. Table 1 gives the results for 1913-'14. Table 2 presents those for 1914-'15.

The average number of eggs laid per month by all birds irrespective of their somatic characters are given for the two years in table 3.

TABLE I

Distribution of birds according to number of eggs laid per month in 1913-1914.

Eggs laid	November	December	January	February	March	April	May	June	July	August	September	October	Annual total
0	126	157	158	21	—	—	—	2	4	9	88	184	749
1	26	9	23	12	—	1	—	2	—	5	26	14	118
2	9	5	6	12	—	1	1	—	2	4	14	10	64
3	21	7	16	12	1	—	—	—	1	4	6	4	72
4	13	3	15	3	2	—	1	1	3	—	6	6	53
5	9	9	10	11	1	—	—	1	2	5	4	4	56
6	13	14	9	21	4	1	—	2	1	3	6	3	77
7	10	9	14	19	1	—	—	2	3	3	8	2	71
8	12	14	5	18	1	—	—	2	2	2	6	7	69
9	9	5	15	24	3	2	—	2	3	4	3	8	78
10	10	7	8	17	2	3	—	4	10	8	4	5	78
11	9	7	5	22	7	4	4	8	8	9	5	8	96
12	12	7	4	16	7	6	3	8	6	4	5	2	86
13	6	5	5	17	14	4	2	6	5	6	6	5	81
14	4	5	7	17	17	8	5	8	9	6	5	3	94
15	10	7	1	22	16	8	3	7	5	8	7	3	97
16	7	6	3	15	26	17	5	7	10	16	11	5	128
17	1	6	2	17	25	15	9	7	11	9	12	10	124
18	1	5	2	8	33	22	15	17	13	17	16	9	158
19	—	7	1	3	32	32	16	19	17	11	18	5	161
20	1	7	—	1	40	47	22	27	27	30	19	8	229
21	—	—	—	1	26	44	27	32	21	24	17	2	194
22	—	5	—	—	27	43	48	31	35	32	11	2	234
23	—	3	—	—	15	31	50	47	38	36	3	—	223
24	—	—	—	—	7	16	41	25	31	36	2	—	158
25	—	—	—	—	1	3	24	24	13	9	1	—	75
26	—	—	—	—	1	1	18	10	21	7	—	—	58
27	—	—	—	—	—	—	—	10	6	1	—	—	23
28	—	—	—	—	—	—	5	2	1	—	—	—	8
29	—	—	—	—	—	—	—	—	1	1	—	—	2
Totals	309	309	309	309	309	309	309	309	309	309	309	309	3708

The differences show how closely the results of the two competitions agreed in their results for mean egg production month by month. Absolutely the differences are small, but relatively they are rather large in comparison with the average egg production of either of the two years, which is of course itself low in the winter months.

It does not seem worth while in this place to consider the magnitudes of these differences in comparison with that of the absolute values upon which they are based or to offer any theories concerning the causes of the observed discrepancies.

That the differences are statistically trustworthy may be seen from the fact that they are often several times as large as their probable errors, as is shown by the final column, in which the ratios have been obtained

TABLE 2

Distribution of birds according to number of eggs laid per month in 1914-1915.

Eggs laid	November	December	January	February	March	April	May	June	July	August	September	October	Annual total
0	152	103	133	47	8	4	3	11	12	25	69	190	757
1	20	14	12	18	1	1	2	2	5	9	16	23	123
2	10	12	16	16	1	—	—	—	1	5	6	14	81
3	16	17	22	15	2	1	1	4	6	3	3	12	102
4	13	13	13	19	2	1	1	—	2	4	5	12	85
5	7	18	15	24	5	4	2	3	2	9	5	13	107
6	18	23	11	21	5	—	1	6	2	1	3	10	101
7	9	17	14	18	8	3	3	4	2	4	4	7	93
8	14	13	15	30	10	2	6	—	3	4	2	8	107
9	14	10	10	18	3	5	8	4	6	8	5	7	98
10	15	15	14	21	13	9	3	5	5	1	6	7	114
11	12	16	11	12	14	7	3	5	5	5	10	4	104
12	18	8	16	20	8	5	2	7	9	7	6	6	112
13	10	11	12	12	16	10	7	7	7	8	12	6	118
14	7	7	8	17	21	25	9	4	9	11	11	7	136
15	13	16	8	21	27	19	6	5	9	8	17	7	156
16	6	12	5	14	23	26	10	4	6	10	20	8	144
17	3	17	14	12	22	30	7	4	11	17	23	8	168
18	4	9	8	12	29	32	13	12	16	24	24	7	190
19	5	12	8	2	39	43	25	12	17	14	25	7	209
20	1	5	6	5	42	39	22	17	22	29	29	6	223
21	6	5	3	1	33	40	45	45	23	36	32	4	273
22	—	1	1	—	15	23	39	41	41	50	16	1	228
23	1	—	—	—	18	25	50	50	36	40	13	1	234
24	—	1	—	—	8	13	42	53	39	25	6	—	187
25	1	—	—	—	1	5	29	33	41	5	6	—	126
26	—	—	—	—	1	2	23	23	25	5	—	—	79
27	—	—	—	—	—	1	10	11	10	3	—	—	35
28	—	—	—	—	—	—	2	2	2	—	1	—	7
29	—	—	—	—	—	—	1	1	1	—	—	—	3
Totals	375	375	375	375	375	375	375	375	375	375	375	375	4500

by dividing the differences by their probable errors.⁴ Thus the performance of the birds at any stated time differed significantly in the two years. Just such differences should be expected. It is perhaps rather surprising that they are not larger. The birds are entirely different series of individuals. The conditions under which the birds were maintained prior to their installation in the contest probably differed somewhat. Finally, while conditions in the two years of the contest are intended to be as nearly as possible the same, it is quite clear that homologous months in two successive winters will rarely be identical in climatic conditions.

⁴ Probable errors have been calculated by the conventional formulae, notwithstanding the abnormal nature of the frequency distributions.

TABLE 3

Mean number of eggs, and probable error of mean number of eggs, laid by all birds for each month.

Month	Mean eggs laid			
	1913-1914	1914-1915	Difference	Diff./E. Diff.
November	4.282 ± .197	5.368 ± .214	+ 1.086 ± .291	3.73
December	5.217 ± .262	7.219 ± .231	+ 2.002 ± .349	5.74
January	3.294 ± .178	6.056 ± .223	+ 2.762 ± .285	9.69
February	9.456 ± .204	8.104 ± .198	- 1.352 ± .284	4.76
March	17.702 ± .155	16.125 ± .188	- 1.577 ± .244	6.46
April	19.405 ± .140	17.701 ± .162	- 1.704 ± .214	7.96
May	21.712 ± .141	20.339 ± .187	- 1.373 ± .234	5.87
June	19.874 ± .198	20.080 ± .223	+ .206 ± .298	.69
July	19.379 ± .224	19.267 ± .239	- .112 ± .327	.34
August	17.919 ± .259	16.848 ± .263	- 1.071 ± .369	2.90
September	9.133 ± .330	12.904 ± .291	+ 3.771 ± .440	8.57
October	4.262 ± .256	4.467 ± .223	+ .205 ± .339	.60

Table 4 gives the variation constants for number of eggs laid per month. Comparisons between the results of the two years may again be made by means of the difference column. Many of the differences are several times as large as their probable errors. Thus the variation in

TABLE 4

Standard deviations and probable errors of standard deviations of number of eggs laid per month by all birds.

Month	Standard deviation of eggs laid			
	1913-1914	1914-1915	Difference	Diff./E. Diff.
November	5.134 ± .139	6.140 ± .151	+ 1.006 ± .205	4.91
December	6.822 ± .185	6.644 ± .164	- .178 ± .247	.72
January	4.639 ± .126	6.408 ± .158	+ 1.769 ± .201	8.80
February	5.316 ± .144	5.687 ± .140	+ .371 ± .201	1.85
March	4.028 ± .109	5.399 ± .133	+ 1.371 ± .172	7.97
April	3.640 ± .099	4.660 ± .115	+ 1.020 ± .152	6.71
May	3.671 ± .100	5.360 ± .132	+ 1.689 ± .166	10.17
June	5.151 ± .140	6.392 ± .157	+ 1.241 ± .210	5.91
July	5.847 ± .159	6.874 ± .169	+ 1.027 ± .232	4.43
August	6.751 ± .183	7.556 ± .186	+ .805 ± .261	3.08
September	8.597 ± .233	8.365 ± .206	- .232 ± .311	.75
October	6.678 ± .181	6.397 ± .158	- .281 ± .240	1.17

egg production in the individual months must be considered to differ significantly in the two experiments. Such differences should be expected for the reasons set forth in the discussion of the means above. The question of the differences between the variabilities at comparable times in the two years or at various times in the same year requires no more detailed discussion here, where the chief value of the standard deviations is to furnish one step towards the correlation coefficients.

Correlation of pigmentation and egg production

Table 5 for 1913-'14 and table 6 for 1914-'15 give the frequency with which birds of different pigmentation classes occur in the two years and the total number of eggs laid by birds of these classes in each month and for the entire year of the two contests. From these totals the mean

TABLE 5

Frequency of birds showing various percentages of yellow and total number of eggs laid by them in each month and during the whole year 1913-1914.

Percent yellow	Number of birds	Total eggs												Annual total
		November	December	January	February	March	April	May	June	July	August	September	October	
10	12	75	108	64	140	234	257	278	247	275	265	224	202	2369
15	34	215	279	176	378	606	665	747	710	746	749	622	456	6349
20	37	220	304	172	402	707	710	848	818	811	759	624	426	6801
25	16	70	68	55	130	261	312	357	345	317	342	262	129	2648
30	20	56	105	86	203	340	342	422	379	390	377	205	64	2969
35	31	94	150	94	329	536	592	638	588	557	548	171	14	4311
40	34	127	134	90	295	591	680	725	634	673	593	219	5	4766
45	39	134	175	72	300	702	766	852	801	730	658	202	9	5401
50	38	132	135	83	327	653	726	808	713	679	597	150	9	5012
55	29	129	120	82	262	521	565	643	572	546	463	107	2	4012
60	13	71	34	44	119	213	264	273	218	203	151	31	—	1621
65	4	—	—	—	35	72	79	83	75	58	35	5	1	443
70	1	—	—	—	—	15	19	12	21	3	—	—	—	70
75	1	—	—	—	2	19	19	23	20	—	—	—	—	83

egg production of birds of a given class may be computed for any period, or data for the determination of the correlation between pigmentation and egg production may be deduced (HARRIS 1910).

Consider first the correlation for October pigmentation and egg production for the entire year.

The nature of the relationship between the concentration of yellow pigment in the ear lobe and the annual egg record of the bird may be most clearly exhibited to the statistically untrained reader by means of

TABLE 6

Frequency of birds showing various percentages of yellow and total number of eggs laid by them in each month and during the whole year 1914-1915.

Percent yellow	Number of birds	Total eggs												Annual total
		November	December	January	February	March	April	May	June	July	August	September	October	
10	1	11	20	3	20	20	19	25	24	22	18	23	10	215
15	29	186	284	241	278	483	551	619	614	622	542	591	409	5420
20	51	332	461	384	449	837	930	1141	1124	1087	1021	975	616	9357
25	24	136	228	192	225	401	417	511	539	515	464	447	270	4345
30	21	116	184	183	168	365	363	452	450	466	420	365	114	3646
35	27	165	203	219	261	469	467	525	534	529	487	428	122	4409
40	32	196	179	158	255	476	525	644	591	564	549	452	48	4637
45	39	182	280	195	317	648	745	798	832	792	728	554	44	6115
50	48	280	296	271	388	769	836	940	919	932	793	455	25	6913
55	44	199	267	193	293	655	748	864	794	682	634	360	4	5703
60	34	118	155	100	237	514	586	629	677	620	395	94	2	4127
65	12	44	70	62	67	188	208	231	226	237	192	67	1	1593
70	11	35	68	70	66	184	199	206	185	157	75	28	—	1273
75	1	—	5	—	8	18	22	19	—	—	—	—	—	72
80	1	4	7	—	7	20	22	23	21	—	—	—	—	104

TABLE 7

Mean number of eggs per year laid by birds showing different percentages of yellow in the two years. The number of birds upon which the averages are based is also shown.

Percent yellow	1913-1914		1914-1915	
	Birds	Mean eggs	Birds	Mean eggs
10	12	197.4	1	215.0
15	34	186.7	29	186.9
20	37	183.8	51	183.5
25	16	165.5	24	181.0
30	20	148.5	21	173.6
35	31	139.1	27	163.3
40	34	140.2	32	144.9
45	39	138.5	39	156.8
50	38	131.0	48	144.0
55	29	138.3	44	129.6
60	13	124.7	34	121.4
65	4	110.8	12	132.8
70	1	70.0	11	115.7
75	1	83.0	1	72.0
80	—	—	1	104.0

the averages of the annual egg production of birds of different pigmentation grades. The results are given in table 7.

The average number of eggs laid per year decreases rapidly from about 200 in birds with 10 percent of yellow to less than 150 in those with over 40-45 percent of yellow in the ear lobes.

The great practical value of the relationship as a means of selecting the best birds may be best seen by grouping these records.

The results are shown in table 7A. Here the birds with 10, 15 and

TABLE 7 A

Percent yellow	1913-1914		1914-1915	
	Birds	Mean eggs	Birds	Mean eggs
10-20	83	187.0	81	185.1
25-35	67	148.2	72	172.2
40-50	111	136.7	119	148.4
55-65	46	132.1	90	126.9
70-80	2	76.5	13	111.5

20 percent yellow are clubbed together, those with 25, 30 and 35 percent form a second group, and so on.

Neglecting the few birds recorded as possessing an unusually high percentage of yellow, i.e., 70-80 percent, it is clear that there are differences of the highest practical significance in the birds constituting the four groups which are sufficiently large to give trustworthy averages. By selecting in October for breeding purposes birds with 10-20 percent yellow, the poultryman will secure a group which have averaged over 30 eggs above the flock as a whole and over 50 eggs above the average of the class with 55-65 percent of yellow. It is to be noted that these differences are not merely very great indeed, but that the group of high-laying birds (10-20 percent yellow) is sufficiently large for economic purposes. Surely eighty birds out of every three or four hundred ought to be a sufficiently liberal number in practical selection operations.

The results may now be expressed in terms of correlation. Summing the products of the total annual egg production, E , by the grades of percentage of yellow, y , for the individual birds, we have

$$\text{For } 1913-14, \Sigma (yE) = 1,603,225$$

$$\text{For } 1914-15, \Sigma (yE) = 2,216,875$$

whence by the formula used (HARRIS 1910),

$$r_{yE} = \frac{\Sigma (yE)/N - \bar{y}\bar{E}}{\sigma_y \sigma_E}$$

where the bars denote the means and the sigmas the standard deviations as given above, we find numerically⁵

$$\begin{aligned} \text{For } 1913\text{'14, } N &= 309 \\ r &= \frac{\Sigma (yE)/N - 36.407769 \times 151.134306}{15.090082 \times 37.853644} = -.5816 \\ \text{For } 1914\text{'15, } N &= 375 \\ r &= \frac{\Sigma (yE)/N - 40.640000 \times 154.477335}{16.078673 \times 43.222447} = -.5271 \end{aligned}$$

Thus the relationship between the October ear lobe pigmentation as measured in units of 5 percent range and the annual egg production of the domestic fowl is surprisingly high.

The differences for the two years in the intensity of the relationship is

$$\begin{aligned} \text{For } 1913\text{'14, } r_{yE} &= -.5816 \pm .0253 \\ \text{For } 1914\text{'15, } r_{yE} &= -.5271 \pm .0252 \\ \hline \text{Difference} & .0545 \pm .0358 \end{aligned}$$

The difference is only about fifty percent larger than its probable error, and cannot be considered statistically significant. Conversely, the results for the two years may be considered practically identical.

The correlation coefficients show on the uniform standard scale of -1 to $+1$ the degree of interdependence of two variables, in this case the percentage of yellow in the ear lobe and the egg record of the domestic fowl. For many purposes measures on such a standard scale are of the highest value. For other comparisons it is desirable to determine not merely the relationship between percentage yellow and egg production on a *relative* scale but also to know just how much birds with different percentages of yellow differ in terms of actual mean number of eggs laid. Such absolute measures have the disadvantage that they are not comparable with measures of the same or other characters taken on the same or any other organism at any other place or time. Thus the two methods supplement each other. Fortunately it is possible to pass at once from relative measures in terms of correlation to absolute values in terms of regression.

⁵ In the calculations involved in this paper all the operations have, of course, been carried to a larger number of places than are given in the tables.

The conventional formula, in terms of the present notation, is

$$E = (\bar{E} - r \frac{\sigma_E}{\sigma_y}) \bar{y} + r \frac{\sigma_E}{\sigma_y} y$$

where E = eggs laid, y = percent yellow, the bars denote the mean values of the characters and the sigmas their standard deviations in the population as a whole.

The actual equations are

$$\text{For 1913-'14, } E = 204.754 - 1.459 y$$

$$\text{For 1914-'15, } E = 212.058 - 1.416 y$$

The second term of the equation shows the *decrease* in annual mean number of eggs laid for each *increase* of one percent of yellow in the ear lobe. Since determinations of yellow are recorded in units of 5 percent range, the second term may be multiplied by five to obtain the actual difference in egg production associated with a difference of one working unit in pigmentation. This will be noted to be about 7 eggs in both years.

These absolute changes may be represented graphically by the slope of a straight line. The points at which such a line cuts the ordinates erected upon the various percentages of yellow, mark off the theoretical mean number of eggs laid by birds of this grade of pigmentation. By theoretical mean number is to be understood merely the mean number which has been calculated from the trend of the data as a whole, on the assumption that the rate of change may be satisfactorily represented by the slope of a straight line. How satisfactorily it can be thus represented is most conveniently determined by a comparison of the theoretical, or smoothed, and the empirical means calculated directly from the data available for the particular class alone.

Such lines are shown for the two years in diagram 3. The actual means from table 7 above are also represented. The agreement of the empirical and theoretical means is not as good as might be wished, but it does not seem desirable on the basis of the present data to consider in any greater detail the precise form of the theoretical line which would best smooth these empirical averages.

Turn now to the interrelationship for the individual months.

The correlations between the percentages of yellow observed in October and egg production for the individual months are given for the two years in table 8.

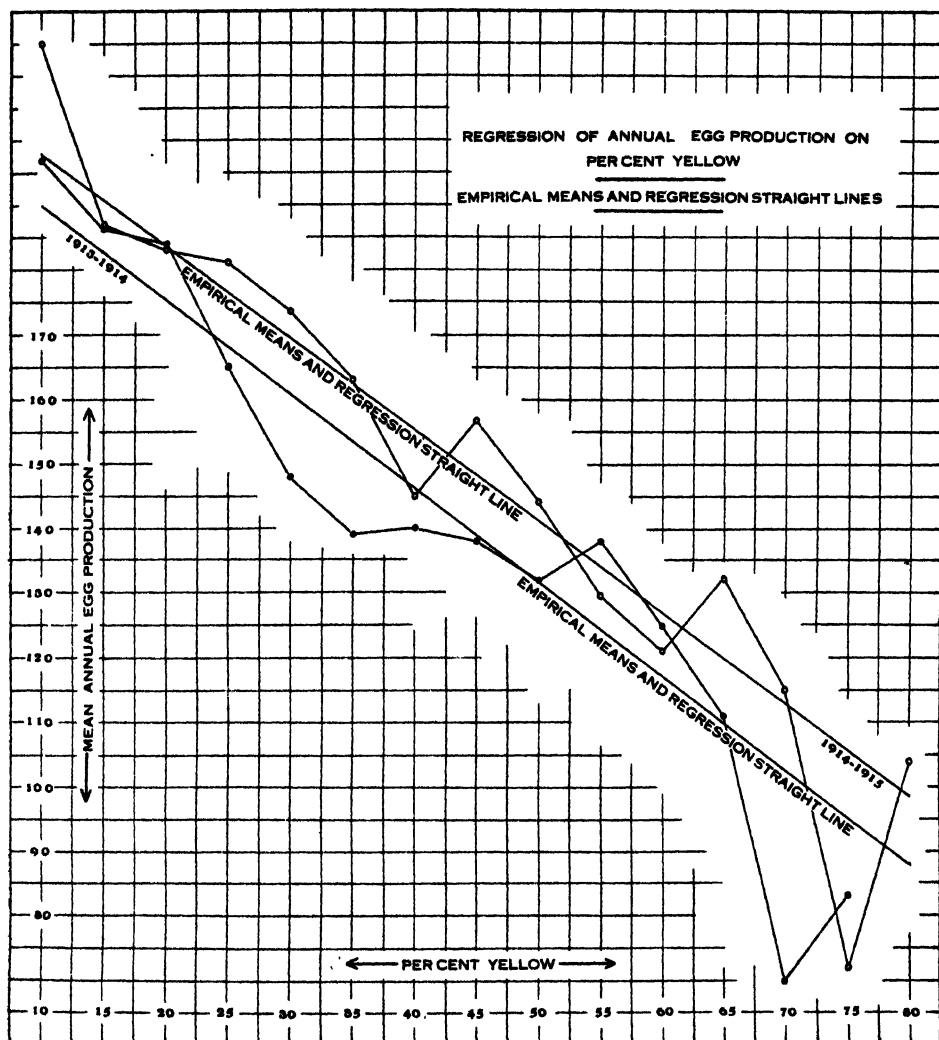


DIAGRAM 3.—Relationship between percent yellow in ear lobes in October and annual egg production. The closed and open circles show the observed mean numbers of eggs laid by birds with varying percentages of yellow. The straight lines represent the equations for the regression of egg production on percent of yellow. They show, on the same ordinates as the empirical averages, the smoothed (theoretical) means calculated from the data as a whole.

Before discussing the absolute magnitudes or the statistical significance of the constants for the individual months, we may draw attention to the consistency of the results for the two years. First of all, it is clear at a glance that although many of the coefficients are low, they are

TABLE 8

Correlations and probable errors of correlations between percent yellow in ear lobes in October and egg production for the individual months of the years, 1913-1914, 1914-1915, and their differences.

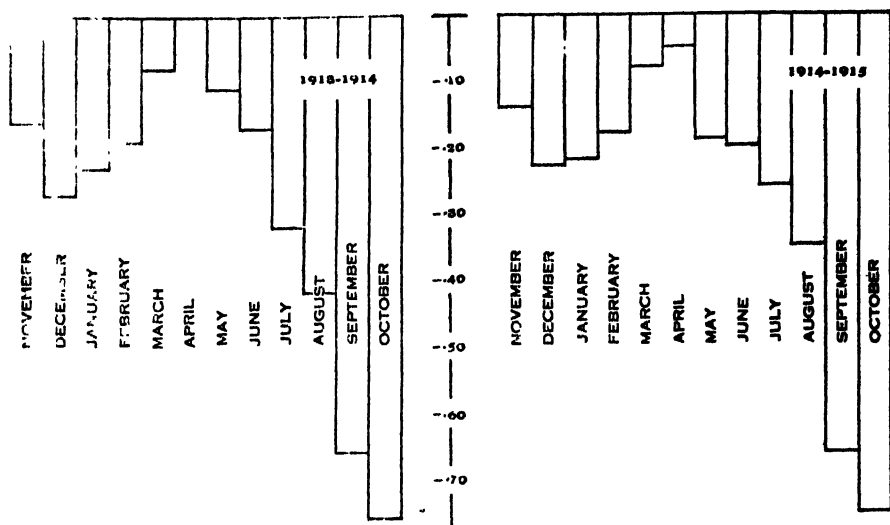
Month	Correlation 1913-1914	r/Er	Correlation 1914-1915	r/Er	Difference in correlation 1913-1914, 1914-1915	Diff./E. Diff.
November	-.167 ± .037	4.51	-.148 ± .027	5.48	-.019 ± .046	0.41
December	-.271 ± .036	7.53	-.230 ± .033	6.97	-.041 ± .049	0.84
January	-.229 ± .036	6.36	-.228 ± .033	6.91	-.001 ± .049	0.02
February	-.193 ± .037	5.22	-.176 ± .034	5.18	-.017 ± .050	0.34
March	-.086 ± .038	2.26	-.080 ± .035	2.29	-.006 ± .052	0.12
April	-.000 ± .038	0.00	-.056 ± .035	1.60	+ .056 ± .052	1.08
May	-.114 ± .038	3.00	-.194 ± .034	5.71	+ .080 ± .051	1.57
June	-.170 ± .037	4.60	-.202 ± .033	6.12	-.032 ± .050	0.64
July	-.324 ± .034	9.53	-.267 ± .032	8.34	-.057 ± .047	1.21
August	-.429 ± .031	13.84	-.354 ± .030	11.80	-.075 ± .044	1.70
September	-.663 ± .022	30.14	-.663 ± .020	33.15	+ .000 ± .030	0.00
October	-.761 ± .016	47.56	-.751 ± .015	50.07	-.010 ± .022	0.45

negative throughout. Comparison of the results for the individual months is facilitated by the column giving the differences and their probable errors. In 8 cases the correlation for 1913-'14 is numerically larger than that for 1914-'15, in 3 cases it is smaller and in one month the coefficients are identical for the first three figures. The absolute magnitude of the differences is of relatively little importance if they are not statistically significant. By dividing these absolute differences by their probable errors, as has been done to obtain the values in the final column of the table, comparable measures of the significance of the differences are obtained. By common consent among statisticians a difference should be at least 2 or 2.5 times as large as its probable error to be regarded as significant—i.e. to be considered to be due to some other cause than the errors of random sampling merely. Of the ratios in this final column not a single one indicates a difference between the coefficients of the two years as much as twice its probable error, only 4 out of the 12 ratios are larger than unity, and the average value is only 0.70. In the discussion of the correlation *for the entire year* it has been shown that the coefficients are, *within the limits of the errors of random sampling*, identical. The results just given show that *in not a single instance can the correlations for the same individual months in the two years be considered to differ significantly*.

We must confess that this result is a matter of some surprise, as well as of gratification to ourselves. Knowing the difficulties of the work and realizing the possible sources of error we were quite prepared to find coefficients distributed with great irregularity and differing by many times their probable errors in the two series of observations. Instead we find results of a higher degree of consistency than are often secured in cases in which theoretically the most refined measurements may be made. A stronger proof of the general accuracy and trustworthiness of our work could not, we believe, be adduced.

As a further means of comparison of the results of the two years, and as a first introduction to the subject of the magnitude of the coefficients for the individual months, diagrams 4 and 5 have been prepared. The two graphs show that the coefficients for the same month in the two years are sensibly identical. They also show that the correlations differ widely from period to period, increasing from the earlier to the later months of the test.

The rate of increase from the first to the last month of the experiment is not, however, uniform. The correlation increases in numerical magnitude from November to December, then it diminishes until it is



DIAGRAMS 4 and 5.—Magnitude of correlation between October ear lobe pigmentation and egg production in the individual months of the two competitions. Distance which the bars extend below the zero line indicates the magnitude of the negative correlations.

practically non-existent in April, after which time it rises rapidly to its maximum value in October. Were there but a single series of data one might suspect the bimodal distribution observed, to be due to chance, but the remarkable agreement of the results for the two years at once throws out this possibility. Furthermore the relation of the constants to their probable errors is such as to leave little doubt concerning the reality of the bimodal nature of the distribution which as a whole shows pronounced skewness. With the exception of the months of March and April only, the constants are three or more times as large as their probable errors. Thus only in April may the correlations be said to be sensibly zero.

Before discussing in detail this question of the differences between the correlations for the various months of the year it seems better to express the results in terms of regression.

The equations appear in table 9. Since yellow is measured in units of five percent range, the amount of change to be expected for a deviation of one working unit has been added in the column headed "change per unit of yellow."

The empirical means for the individual months are calculated from the frequencies and total egg productions recorded in tables 5 and 6. The results are shown for the first three months, November, December

TABLE 9

Straight line equations showing the regression of number of eggs laid per month upon October ear lobe pigmentation.

Month	1913-1914		1914-1915	
	Regression equation	Change per unit* of yellow	Regression equation	Change per unit* of yellow
November	$E = 6.355 - .057 y$.29	$E = 7.664 - .057 y$.29
December	$E = 9.677 - .122 y$.61	$E = 11.083 - .095 y$.48
January	$E = 5.860 - .070 y$.35	$E = 9.755 - .091 y$.46
February	$E = 11.937 - .068 y$.34	$E = 10.628 - .062 y$.31
March	$E = 18.543 - .023 y$.12	$E = 17.219 - .027 y$.14
April	$E = 19.405 - .000 y$.00	$E = 18.359 - .016 y$.08
May	$E = 22.723 - .028 y$.14	$E = 22.965 - .065 y$.33
June	$E = 21.987 - .058 y$.29	$E = 23.343 - .080 y$.40
July	$E = 23.942 - .125 y$.63	$E = 23.902 - .114 y$.57
August	$E = 24.907 - .192 y$.96	$E = 23.605 - .166 y$.83
September	$E = 22.890 - .378 y$	1.89	$E = 26.923 - .345 y$	1.73
October	$E = 16.527 - .337 y$	1.69	$E = 16.612 - .299 y$	1.50

* Unit = 5 percent.

and January, in diagram 6, for the months February, March and April in diagram 7, for the months May, June and July in diagram 8, for August in diagram 9, for September in diagram 10, and for October in diagram 11.

In these graphs the varying slope of the lines indicates the amount of change in egg production associated with variations of the amount indicated in the percentage of pigment. Since all are drawn to the same scale direct comparisons between them are possible. It is clear, for example, that the rate of change decreases from the first winter months of the experiment to April, when the line shows practically no slope and that it again increases until, in the late summer and early autumn months of August, September and October, the slope of the lines is very steep indeed. All this may be seen from the tables. The diagrams further show—and this is their greatest value—that for all the months excepting October, a straight line furnishes as good a graduation as could be expected from any curve of a higher order. To be sure there is great irregularity in the distribution of the empirical means about the theoretical means given by the straight line, but such discrepancy is regularly and necessarily found as a result of random sampling when

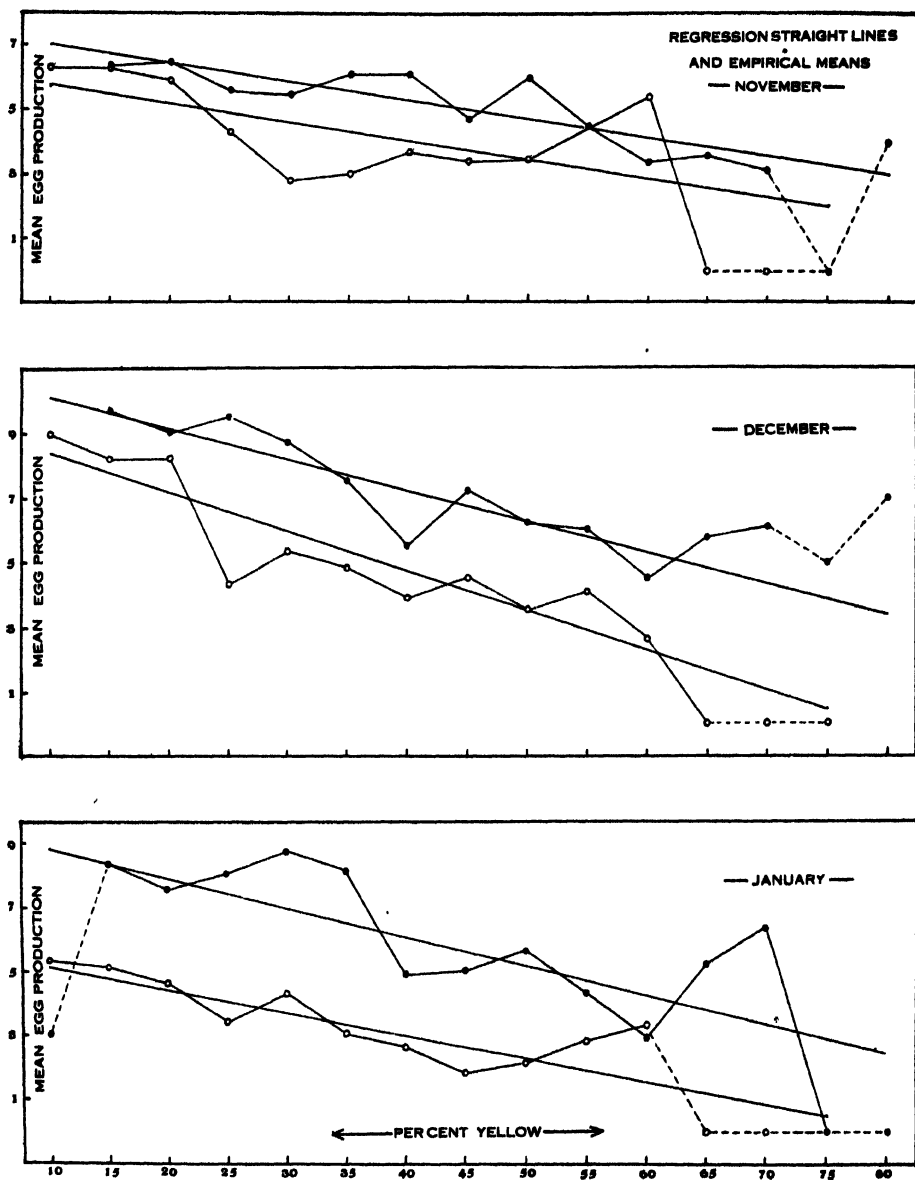


DIAGRAM 6.—Regression of egg production on percent yellow in ear lobes in October for the individual months November, December and January. Compare explanation of diagram 3.

the number of observations is not large and correlation is of a low order of magnitude.

To the exception to the rule of a sensibly linear relationship between

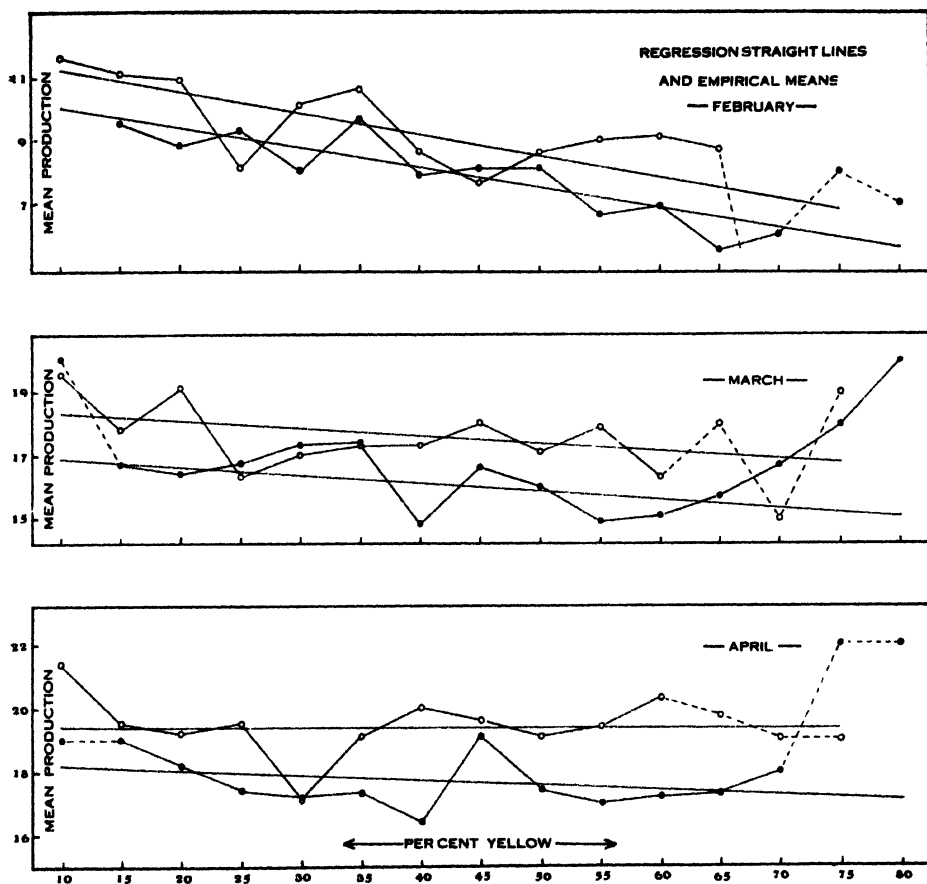


DIAGRAM 7.—Regression of egg production on percent yellow in ear lobes in October for the individual months February, March and April.

percentage of yellow and egg record we shall return in a subsequent section.

The maximum rates of change are found in the winter and autumn months. Thus in December there is a decrease of about half an egg for each increase of 5 percent in October pigmentation. In August, September and October the change is much greater. In March, April and May it is at a minimum.

ATTEMPTED ANALYSIS OF OBSERVED INTERRELATIONSHIPS

In this section we shall attempt by the means of further analysis to interpret certain of the relationships established in the foregoing pages.

One of the most suggestive peculiarities of the measures of inter-

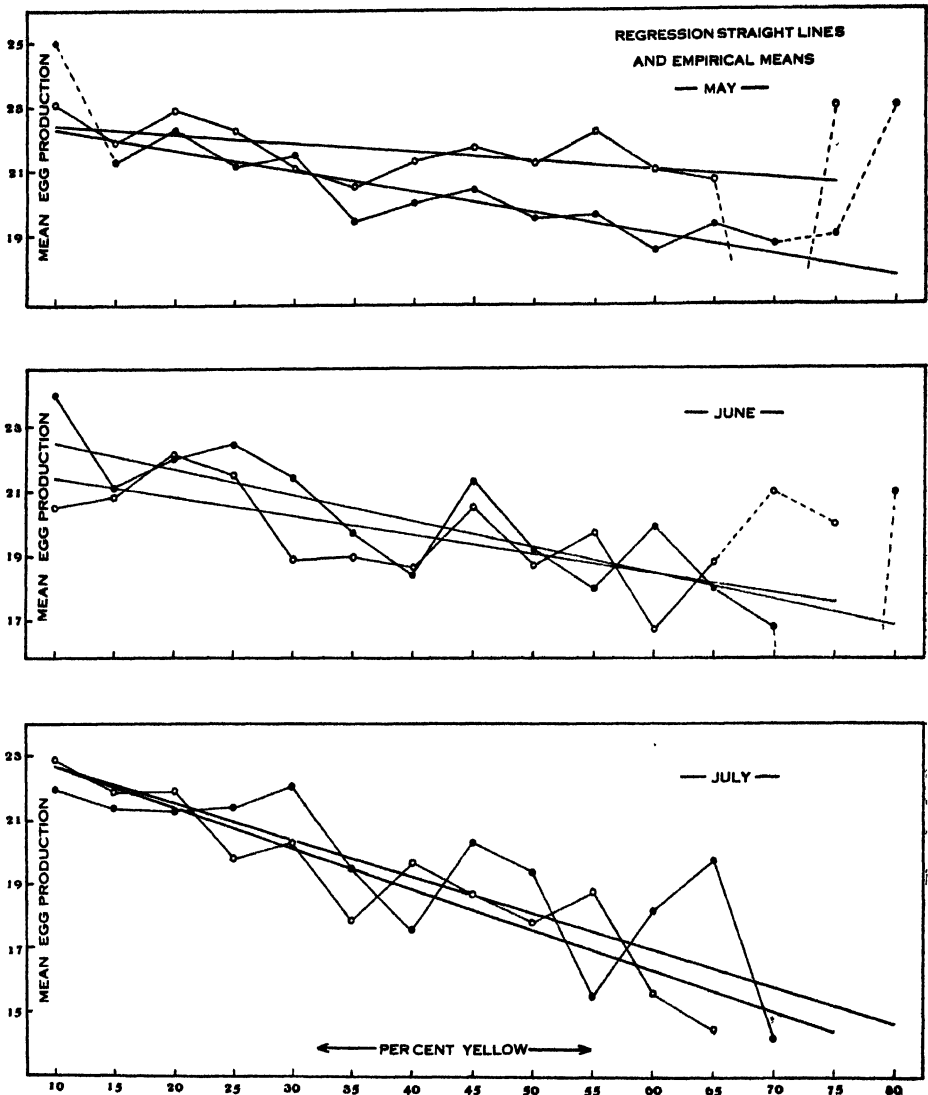


DIAGRAM 8.—Regression of egg production on percent yellow in ear lobes in October for the individual months May, June and July.

dependence of pigmentation and egg production is the difference in the intensity of this relationship exhibited by the several months of the year. If the relationship between pigmentation and egg production be a purely physiological one, at least in some of its essentials, one might expect that the highest correlations would be those determined when the two variables are closely associated in time. This has been shown to be, roughly speaking, the case. It is perfectly clear from the correlations

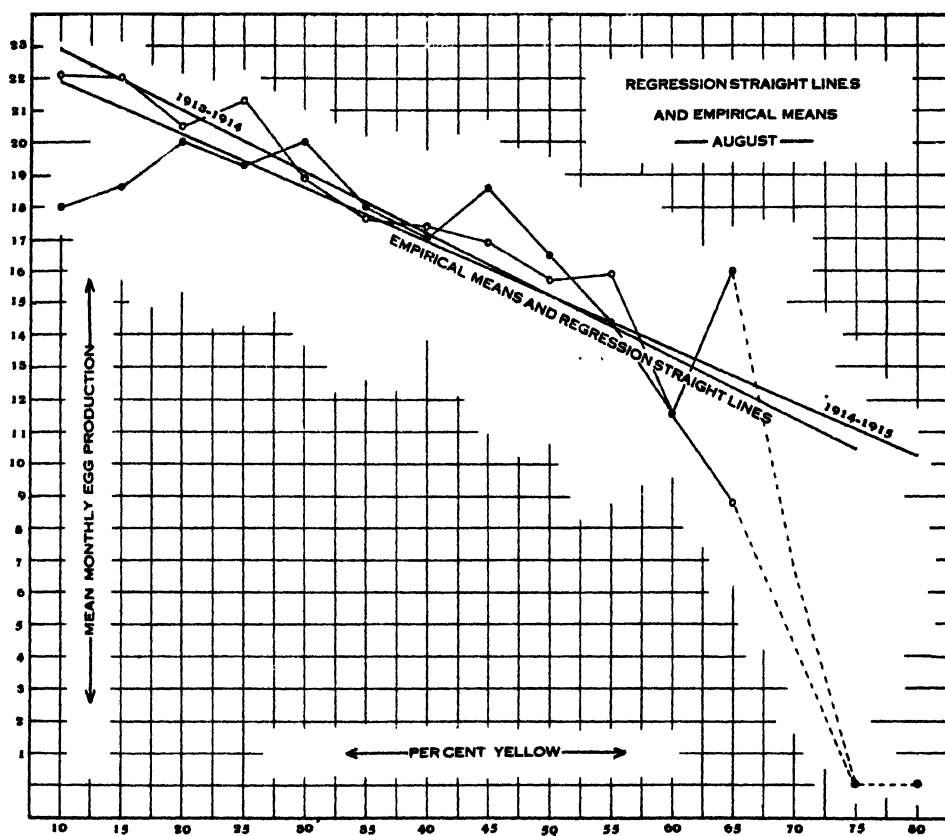


DIAGRAM 9.—Regression of egg production on percent yellow in October for the month of August.

given in table 8, from the regressions shown in table 9, or from the correlations represented in diagrams 4 and 5, or the regressions shown in diagrams 6 to 11, that the numerical magnitude of the interdependence increases toward the end of the experiment. To avoid any possible confusion the reader must always bear in mind that the pigmentation determinations were taken at the end, and (unfortunately) only at the end, of the egg-laying contest.

A priori the most logical hypothesis to account for the relationship observed would seem to be that the growth of the egg abstracts certain substances—in the present case the pigment—from the body tissues with a resulting negative correlation between egg production and quantity of pigment present. This would at once account for the generally

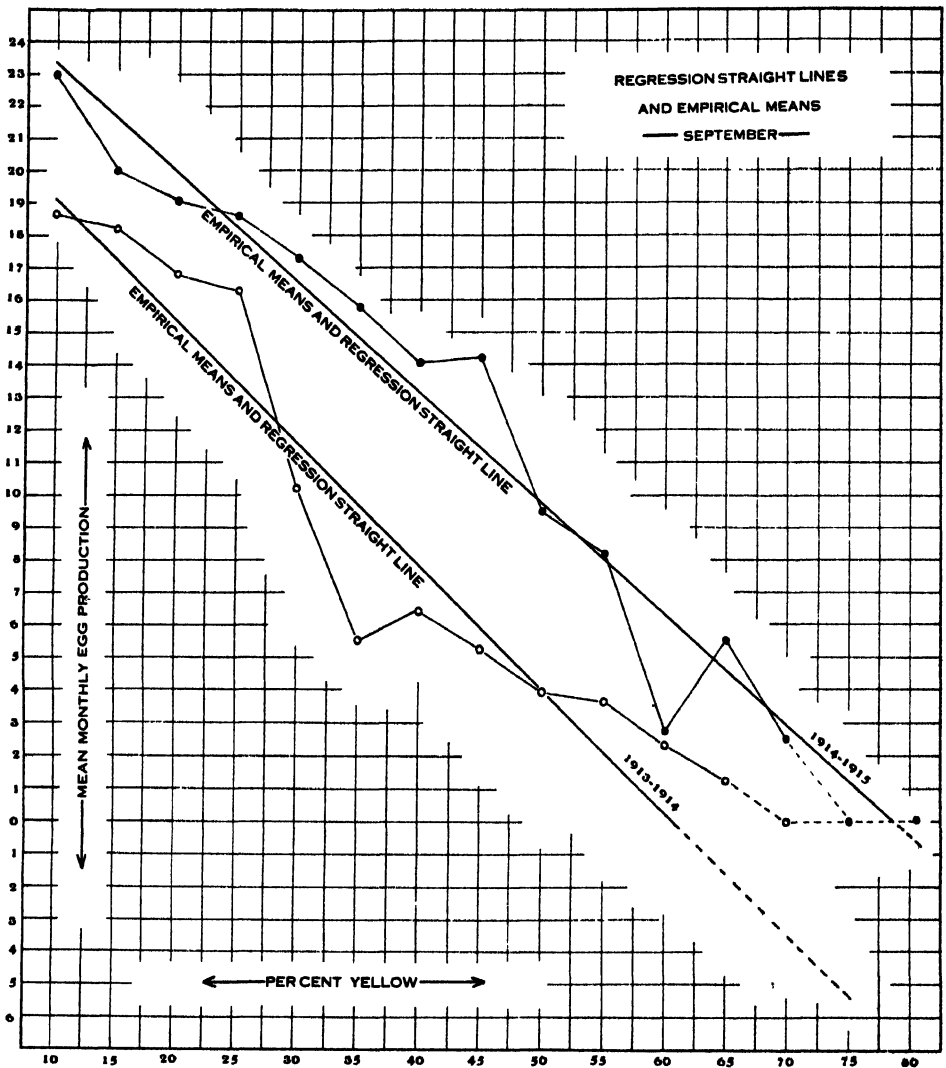


DIAGRAM 10.—Regression of egg production on percent yellow in October for the month of September.

higher correlation between measures made at more closely associated periods of time. If this hypothesis be true, one would expect the maximum correlation to come in or near whatever month the pigment determinations were made.

If this view be the correct one, the (relatively) independent variable would be egg production, the dependent variable would be pigmentation. Egg production would then be looked upon, provisionally at least, as the

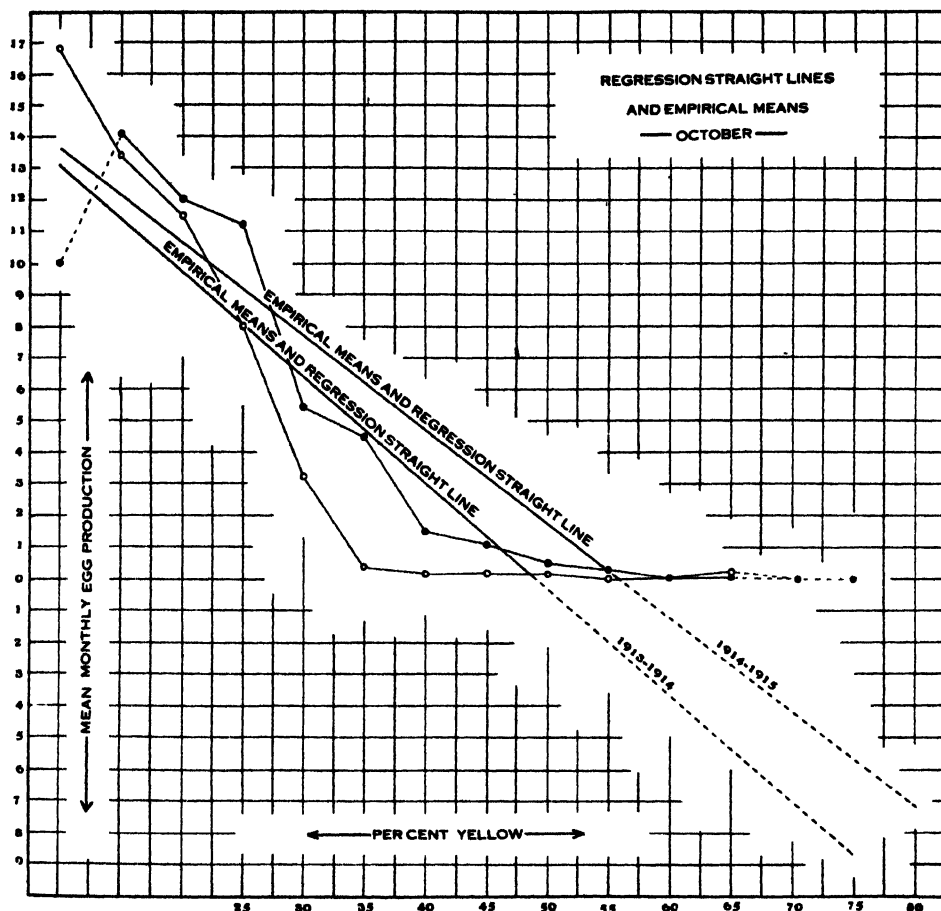


DIAGRAM 11.—Regression of egg production in October on the percent yellow in the ear lobes in the same month.

(chief) proximate cause of the observed intensity of pigmentation. Heretofore in this paper pigmentation has apparently been taken as the more fundamental character. This was not because we believed it to be so *physiologically*, but because we have been seeking to determine the prediction value of a somatic character for use in the selection of birds with a high egg record without actually determining that record by trap-nesting.

Bearing these considerations in mind it is most instructive to compare the distribution of yellow among the birds with different egg records when the egg records are taken in the same month as the pigmentation

TABLE 10

Percent yellow in October 1914 and egg production in November 1913.

		October, 1914, pigmentation															Totals
		10	15	20	25	30	35	40	45	50	55	60	65	70	75		
November, 1913, egg production	0	3	12	8	4	9	17	14	17	21	13	2	4	1	1	126	
	1		2	7	2	3	1	3	2	3	1	2				26	
	2	3	1		1		2			2						9	
	3			2	3	3	3	4	3	2		1				21	
	4			1				2	6	1	1	2				13	
	5			2	1			1	1		2	2				9	
	6		2	1	2	1	1	2	1		1	2				13	
	7		1	1			3	1	2		2					10	
	8		3	2		1			2	2	2					12	
	9	1	1			2		3			2					9	
	10		2	4	1				2		1					10	
	11	1	2				1	1	1	1	2					9	
	12	3	2	2	1	1	1	1	1							12	
	13	1		3						1	1					6	
	14			1			1	1		1						4	
	15		3	2					1	3	1					10	
	16		3				1	1		1		1				7	
	17			1												1	
	18				1											1	
	19															0	
	20											1				1	
Totals		12	34	37	16	20	31	34	39	38	29	13	4	1	1	309	

determinations and when the two determinations are separated by a wide interval of time.

The tables for November egg production and October pigmentation represent the most widely separated records. Those for October egg production and October pigmentation represent the most closely associated measurements of the two characters. These two months are, furthermore, particularly suited to our present purposes because in each case a very high and fairly similar percentage of the birds laid no eggs at all. The percentages of birds which laid no eggs are:

	November	October
1913-'14	40.78	59.87
1914-'15	40.53	50.67

For the remaining fecundity classes, the range of variation and the distribution of the frequencies as shown by the total columns are very similar.

TABLE II

Percent yellow in October 1914 and egg production in October 1914.

		October pigmentation														Totals
October egg production		10	15	20	25	30	35	40	45	50	55	60	65	70	75	
	0			2	3	10	25	32	34	33	28	13	3	1	1	185
	1			1	2		2	1	3	3			1			13
	2		1	1		3	2		1	1	1					10
	3			1		1	1			1						4
	4		1	1	1	1		1	1							6
	5		1	2			1									4
	6			2		1										3
	7				1	1										2
	8		2	2	1	2										7
	9		3	4	1											8
	10	1	2	1	1											5
	11		4	2	2											8
	12			1	1											2
	13	2	1		1	1										5
	14		3													3
	15	1		2												3
	16		2	1	1	1										5
	17	2	3	5												10
	18	2	5	1	1											9
	19	2	2	1												5
	20		3	4	1											8
	21	1		1												2
	22	1		1												2
Totals		12	34	37	10	20	31	34	39	38	29	13	4	1	1	309

The distribution of the birds in the bodies of tables 10 and 11 for 1913 and of tables 12 and 13 for 1914-'15, is however very different. In the case of the November production for each year the birds of all the different fecundities are scattered with a fair degree of uniformity over the whole range of pigmentation. In October, however, the birds which have laid no eggs at all show a distribution of yellow pigmentation which is far more heavily represented in the higher classes of yellow than are those which are laying. Furthermore it is quite evident from these tables that in October, pigmentation decreases very rapidly as one passes from birds which have laid no eggs to those which have laid 1, 2, 3 or more eggs, but that this decrease soon falls off so that birds which have laid over about 6 or 7 eggs are apparently sensibly alike in the amount of yellow which they exhibit.

The same point may of course be shown by computing the average percent yellow for birds of each class with respect to egg production. These are shown in diagrams 12 and 13.

TABLE 12

Percent yellow in October 1915 and egg production in November 1914.

		October, 1915, pigmentation																Totals
		10	15	20	25	30	35	40	45	50	55	60	65	70	75	80		
November, 1914, egg production	0		10	16	8	6	11	12	17	19	20	21	7	4	1		152	
	1			1	2	3		2	2	3	2	1	1	3			20	
	2			1	1	1	2		1	1	1	1		1			10	
	3			1	3	2	1	2	2	3	1		1				16	
	4				2		1	1	1	1	1	3		1	1		13	
	5				3			1		1		1	1				7	
	6			2	2	2	1		3	1	2	4	1				18	
	7				3			2	1		1	1	1				9	
	8			2	3	2		1		3	1	2					14	
	9			2	2			1	2	2	4	1					14	
	10			4	2	1	1			1	2	2	2				15	
	11	1		2	1	1			1	1	3		1	1			12	
	12			1	2		2	3	2	1	3	3			1		18	
	13			1	4	1	1					1	1	1			10	
	14							2	1	1	1		1			1	7	
	15			2	1	1	1	2		2	1	1	1	1			13	
	16				1	2	1		1		1						6	
	17					1			1	1							3	
	18			1			1		1	1							4	
	19				1						2	2					5	
	20								1								1	
	21				2				1		2		1				6	
	22																0	
	23				1												1	
	24																0	
	25							1									1	
Totals		1	29	51	24	21	27	32	39	48	44	34	12	11	1	1	375	

The straight lines in these diagrams are calculated from the equations:

For November, 1913, $y = 38.514 - 0.492 e$

For October, 1914, $y = 43.740 - 1.720 e$

For November, 1914, $y = 42.720 - 0.388 e$

For October, 1915, $y = 49.073 - 1.888 e$

The minus quantities in these equations show that *if the rate of change in pigmentation were uniform from the lowest to the highest layers*, which it is not in October, the yellow decreases less than half a percent for each additional egg laid by a bird in November, but about one and three quarters percent for each egg laid in October.

It is quite clear that in the case of the November egg records the percent yellow changes but slowly and irregularly with egg production,

TABLE 13

Percent yellow in October 1915 and egg production in October 1915.

		October pigmentation																Totals
		10	15	20	25	30	35	40	45	50	55	60	65	70	75	80		
October egg production	0			3	2	5	10	19	22	35	37	33	11	11	1	1	190	
	1					2		4	8	5	3		1				23	
	2			1			1	2	1	6	2	1					14	
	3			1				4	1	4	1	1					12	
	4		1	1	2	2	4		1		1						12	
	5		1	3		4	2	1	1	1							13	
	6			3	1	1	1	3	1								10	
	7			1		3		2	1								7	
	8		5	1	2												8	
	9		1	2	3		1										7	
	10	1	1	3	1	1											7	
	11			3	1												4	
	12		1	2	2	1											6	
	13		2	3	1												6	
	14		3	2	2												7	
	15		3	2	1		1										7	
	16			4	2	1	1										8	
	17		1	5	1		1										8	
	18		2	5													7	
	19		3	2		1	1										7	
	20		1	4	1												6	
	21		3		1												4	
	22				1												1	
	23		1														1	
Totals		1	20	51	24	21	27	32	39	48	44	34	12	11	1	1	375	

whereas in the October series the yellow pigment falls very rapidly at first, but thereafter remains practically uniform up to the highest egg classes.

The biological inference to be drawn from this result would seem to be that the egg production of a recent period influences very profoundly the concentration of yellow pigment, so that there is a very rapid decrease in yellow pigment for each additional egg laid, up to a certain point, beyond which the body pigment is relatively little reduced by extra egg production. Thus for October the change in pigmentation is to be described by a curve, not by the slope of a straight line. The change in pigmentation is not proportional to egg production, but at first is very rapid and then falls off.

The point has been investigated in a somewhat different manner in our preliminary paper (BLAKESLEE and WARNER 1915 a, b). There a table is given showing the distribution of 932 records made on 317

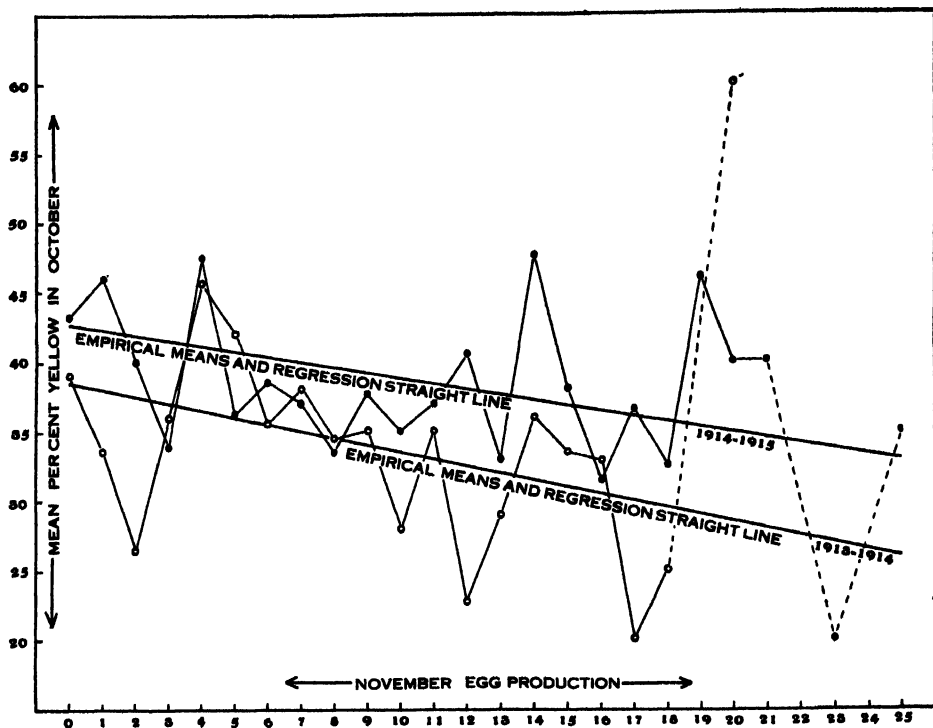


DIAGRAM 12.—Regression of percent of yellow in ear lobes in October on egg production of the *preceding* November. The closed and open circles show the mean percentage of yellow in October for birds laying various numbers of eggs in November. Note the very gentle slope of the lines and the great irregularity in the distribution of the empirical means. Compare diagram 13.

White Leghorns in three series of observations in October of the 1913-'14 competition. The records summarized in this table were made to show the length of time since laying for birds of the various pigment grades. In collecting these data a bird which laid on the day the pigment determination was made or on a later day within the month was considered to be laying, and was recorded in the zero class, i.e., no days since laying. If she laid on the day before the record was taken but not later she is recorded as one day since laying, and so on.

In the table, the results of which are represented graphically in diagram 14, the data are treated in two ways. First of all, the percentage of the birds of various pigmentation classes which are "laying" or "not laying" at the time the color determinations were made, is given. These are represented by the ordinates connected by the light line in the diagram. The percentage of the birds which are laying falls precipitously

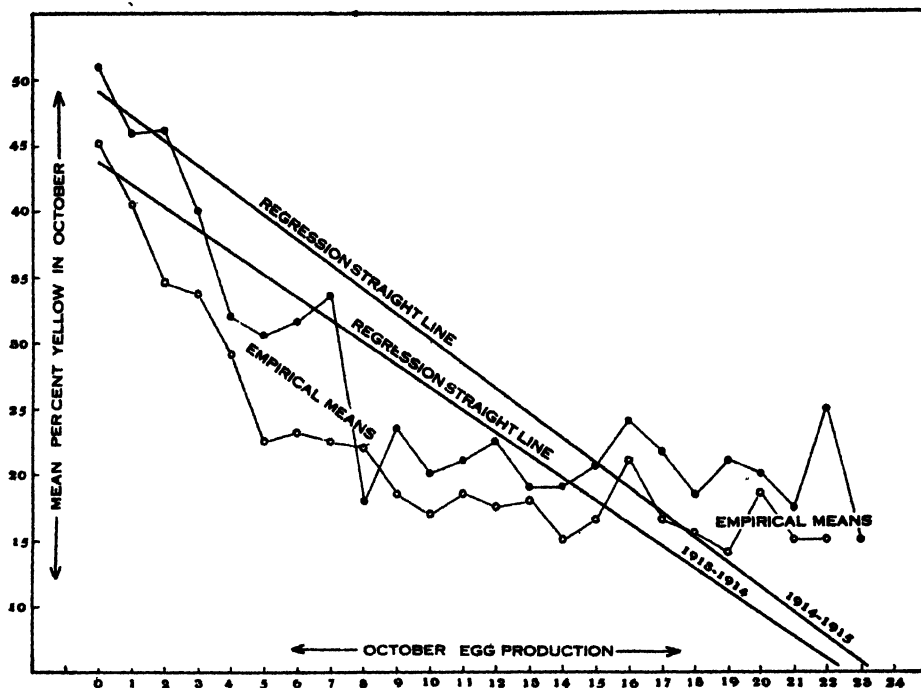


DIAGRAM 13.—Regression of percent of yellow in ear lobes in October on egg production for the same month. Note that as egg production increases the mean percentage of yellow decreases very rapidly, not slowly as in the case of the regression of October pigmentation on the egg production of the preceding November as shown in diagram 12. Note also that the change in percent of yellow is not a uniform one, as is approximately true in the case of the relationship shown in diagram 12, but that the rate of decrease falls off as the heavier-laying classes of birds are reached.

from 87.8 percent among those showing only 6-10 percent yellow, to practically zero for all grades of yellow above 30 percent.⁶

The average number of days since laying has also been computed. This is shown by the heavy line in the diagram. Beginning with an average of only .4 day since laying, in the 6-10 percent color class, the average length of time since laying increases rapidly. Probably the irregularity just before the upper limit of 71 days is due to the small number of records.

⁶ The three cases of laying, among 557 records, in the grades above 30 percent yellow were for sporadic layers. The one in the 40 percent group laid October 18, but at no other time in October or September. This case may perhaps be an error in the egg record. One of the two in the 50 percent grade laid during October only on the 2nd, 4th and 25th, though she laid 18 eggs in September; the other laid during October only on the 16th and 19th and had no eggs to her credit in the second half of September.

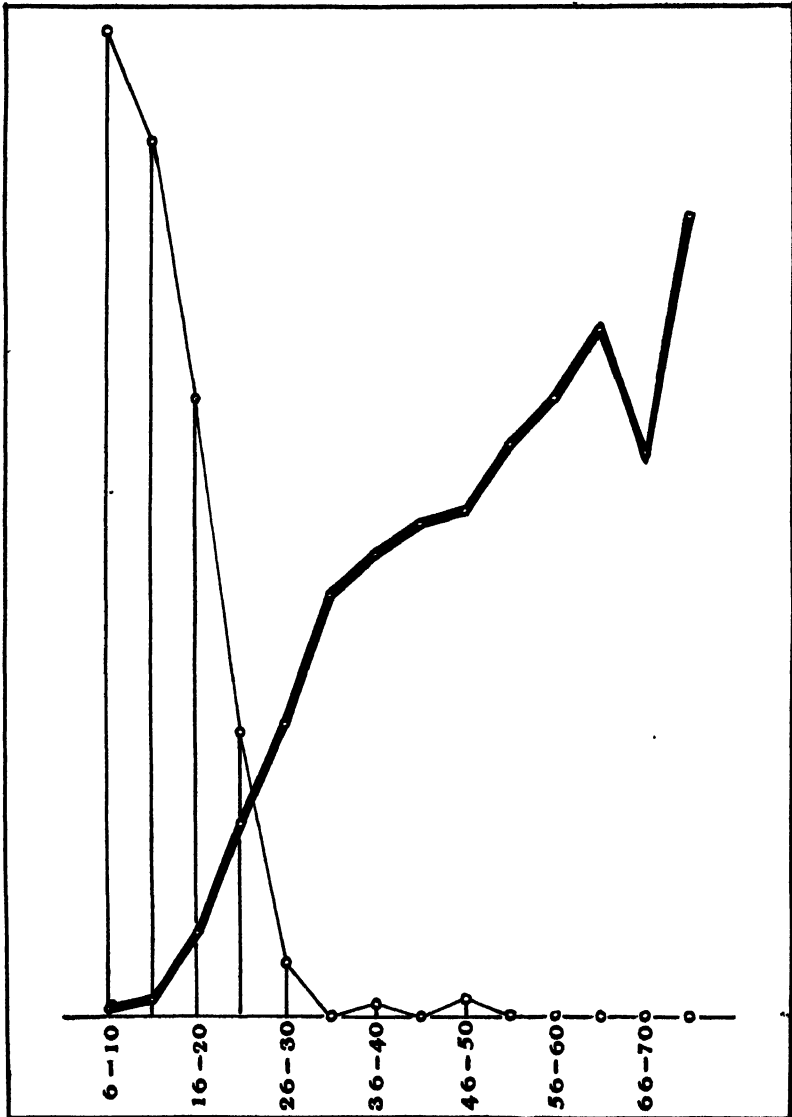


DIAGRAM 14.—Percentage of birds which are laying (light line) and mean number of days since laying (heavy line) in birds with different grades of ear lobe pigmentation.

We now turn to a different aspect of the problem.

If the relationship between percentage of yellow and egg production be chiefly of a physiological nature, it is quite conceivable that the correlations between the October percentage of yellow and egg production during the earlier months of the experiment, may be largely the resultant of other interrelationships. Let us consider this possibility in detail.

Yellow pigment is closely correlated with October egg production. Inspection of the values of the correlation coefficients for percentage yellow and egg production of the individual months shows that the correlation decreases as the monthly egg record becomes farther distant in time from the date of color determination. The decrease is not a uniform one.

If the October egg production of a bird be correlated with her egg production for each of the preceding months of the experiment, then these two interrelationships would tend to bring about a correlation between October pigmentation and the egg production of every other month in the year.

A quantitative measure of the influence of this factor may be secured as follows:

Let $r_{ye_1}, r_{ye_2}, r_{ye_3} \dots r_{ye_{12}}$ be the correlations between percent yellow in the twelfth month of the contest and egg production in the first, second, third ... twelfth months respectively. Further let $r_{e_{12}e_1}, r_{e_{12}e_2}, r_{e_{12}e_3} \dots r_{e_{12}e_{11}}$ be the correlations between October and November, October and December, October and January ... October and September egg productions. If now the values of $r_{ye_1}, r_{ye_2}, r_{ye_3} \dots r_{ye_{11}}$ be in large part the resultants of $r_{e_{12}e_1}$ and $r_{ye_{12}}, r_{e_{12}e_2}$ and $r_{ye_{12}}, r_{e_{12}e_3}$ and $r_{ye_{12}} \dots r_{e_{12}e_{11}}$ and $r_{ye_{12}}$, material reductions in the values of $r_{ye_1}, r_{ye_2}, r_{ye_3} \dots r_{ye_{11}}$ should result from the rendering constant of the variable e_{12} . Hence applying the well known partial correlation formula for one variable, e_{12} , constant we have:

$$\begin{aligned} c_{12} r_{ye_1} &= \frac{r_{ye_1} - r_{ye_{12}} r_{e_{12}e_1}}{\sqrt{1 - r_{ye_{12}}^2} \sqrt{1 - r_{e_{12}e_1}^2}}, \\ c_{12} r_{ye_2} &= \frac{r_{ye_2} - r_{ye_{12}} r_{e_{12}e_2}}{\sqrt{1 - r_{ye_{12}}^2} \sqrt{1 - r_{e_{12}e_2}^2}}, \\ c_{12} r_{ye_3} &= \frac{r_{ye_3} - r_{ye_{12}} r_{e_{12}e_3}}{\sqrt{1 - r_{ye_{12}}^2} \sqrt{1 - r_{e_{12}e_3}^2}}, \\ &\vdots \\ c_{12} r_{ye_{11}} &= \frac{r_{ye_{11}} - r_{ye_{12}} r_{e_{12}e_{11}}}{\sqrt{1 - r_{ye_{12}}^2} \sqrt{1 - r_{e_{12}e_{11}}^2}}. \end{aligned}$$

The evaluations of these equations require merely the calculation of 24 new correlations, the values of $r_{e_{12}e_1}$, $r_{e_{12}e_2}$, \dots $r_{e_{12}e_{11}}$ for the two years. These constants are given in table 14. They are positive throughout, indicating that birds which excelled in egg production in October gave on an average higher productions in every other month of the year. The intensity of the correlations, however, varies greatly from the first to the eleventh month. This point does not, however,

TABLE 14

Correlation between October egg production and the egg production of the other eleven months of the year.

Correlation between October and:	1913-1914	1914-1915	Differences	Diff./E. Diff.
November	.219 \pm .037	.139 \pm .034	-.080 \pm .050	1.60
December	.333 \pm .034	.253 \pm .033	-.080 \pm .047	1.70
January	.255 \pm .036	.236 \pm .033	-.019 \pm .049	.39
February	.219 \pm .037	.207 \pm .033	-.012 \pm .050	.24
March	.139 \pm .038	.130 \pm .034	-.009 \pm .051	.18
April	.043 \pm .038	.116 \pm .034	+.073 \pm .051	1.43
May	.207 \pm .037	.217 \pm .033	+.010 \pm .050	.20
June	.265 \pm .036	.170 \pm .034	-.095 \pm .050	1.90
July	.326 \pm .034	.271 \pm .032	-.055 \pm .047	1.17
August	.365 \pm .033	.305 \pm .032	-.060 \pm .046	1.30
September	.694 \pm .020	.570 \pm .023	-.115 \pm .030	3.83

especially concern us in this place. The results for the two years are very closely similar. In only one case is the difference between the coefficient obtained for the 1913-'14 and the 1914-'15 competition twice as large as its probable error. The results are generally lower in 1914-'15 than in the first of the two competitions.

Inserting these values (kept to a larger number of decimal places) in the above equations, we find the results set forth in table 15.

The results are also represented graphically in diagrams 15 and 16. Here the bars on the negative side of the zero bar indicate by their lengths the magnitude of the (negative) correlation between October pigmentation and egg production for the 12 individual months of the year. In this feature the diagram is merely a repetition of diagrams 4 and 5, above. The shaded areas superimposed upon these are the partial correlation coefficients from table 15.

The magnitudes of the interrelationships have been very greatly reduced by correcting for variable egg production in October. Since the correlation so nearly disappears in the early months when correction is made for October egg record, it seems reasonable to conclude that the correlation between yellow pigment in October and egg production in the earlier months of the year cannot be looked upon as indicating that there are strains of birds characterized by lighter pigmentation that are better layers, and that a mixture of all these strains in the flock results

TABLE 15

Partial correlations and probable errors of October pigmentation and egg production in remaining eleven months for constant October egg production.

Month	Partial correlation and probable error	
	1913-1914	1914-1915
November	-.001 \pm .038	-.067 \pm .035
December	-.020 \pm .038	-.064 \pm .035
January	-.056 \pm .038	-.079 \pm .035
February	-.042 \pm .038	-.031 \pm .035
March	+.030 \pm .038	+.027 \pm .035
April	+.051 \pm .038	+.048 \pm .035
May	+.068 \pm .038	-.048 \pm .035
June	+.051 \pm .038	-.114 \pm .034
July	-.123 \pm .038	-.099 \pm .035
August	-.251 \pm .036	-.199 \pm .033
September	-.280 \pm .035	-.424 \pm .029

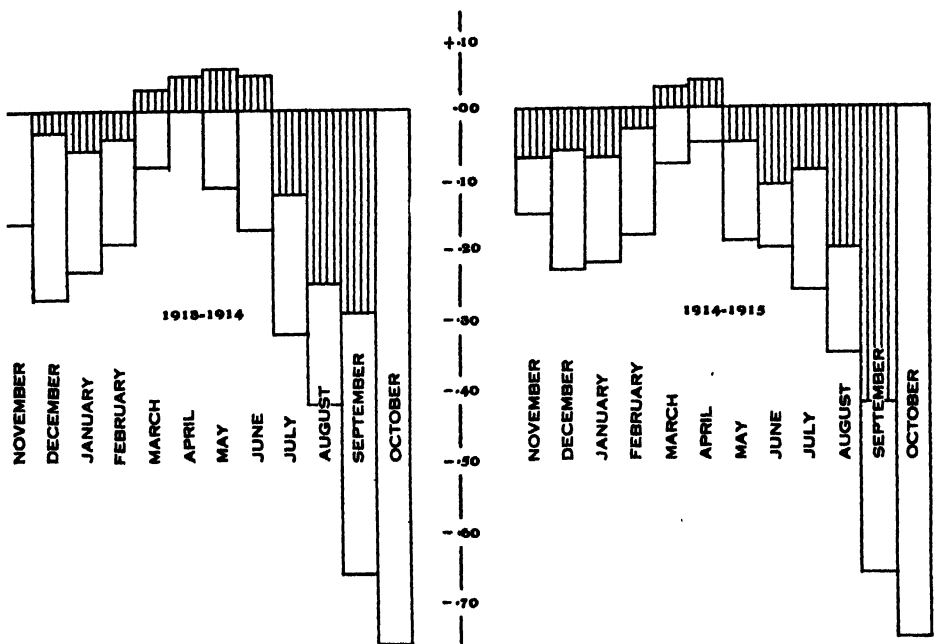
in correlations of the kind which we have demonstrated. The indications are rather that egg production in the earlier months is related to October pigmentation because the birds which are better layers in the early months are also better layers in the fall months, and because October egg production is closely correlated with October pigmentation.

That the correction for October egg production should not so nearly eliminate the correlation between October pigmentation and the egg production of the immediately preceding months, say August and September, is perhaps due to the fact that eggs developed and laid in these months or developed in these months and laid in a subsequent month, must—if the purely physiological theory be the correct one—influence profoundly the pigmentation measured in October.

BIOLOGICAL HYPOTHESES IN EXPLANATION OF THE
OBSERVED CORRELATIONS

While the primary purpose of this paper has been the presentation of data and the statistical constants showing the relationship between body pigmentation (ear lobe pigmentation only, in the present paper) and egg production deduced from them, it is proper to refer briefly to the underlying physiological causes of the demonstrated relationships.

The simplest hypothesis is, as pointed out above, that in heavy laying the large quantity of yolk substance produced removes the yellow pig-



DIAGRAMS 15 and 16.—Correlations between October pigmentation and egg production for individual months (unshaded polygon) and partial correlations between October pigmentation and egg production for the individual months (shaded polygon). In the partial correlations, the influence of the correlation of the egg production of November to September with that of October upon the correlation of the egg record for November to September with October pigmentation is eliminated.

ment from the somatic tissue more rapidly than it can be replaced. This is the suggestion offered in an anonymous press letter (1914) from the MAINE AGRICULTURAL EXPERIMENT STATION and by BLAKESLEE and WARNER (1915 a, b).

Since we have been unable to contribute purely chemical data to the problem, it will be sufficient to point out merely that such observations

as have been reported by others from the field of physiological chemistry are quite consistent with the above view.

The nature of the pigment of the ear lobe of the domestic fowl has not been directly demonstrated, but BARROWS (1914) finds that the yellow shank color is due to yellow fat deposits in the Malpighian layers of the epidermis. It seems most reasonable to consider the color of the ear lobe due to an identical fat-soluble pigment.

While concerned primarily with the problem of fat deposition in, and fat absorption from, the egg, RIDDLE (1911, pp. 475-476) in discussing the mechanism of pigment deposition, says:

"As a concluding word on the rôle of the partition coefficient we record our belief that it alone accounts for the presence of the yolk coloring matter—vitello-lutein and vitello-rubin—in the yellow yolk and not in the white. These are lipochrome pigments, soluble only in fat and fat solvents and are abundant in the large yolk spherules, probably because, as we have shown by comparative analyses, these spherules abound in fat."

Turning now to the more purely chemical literature it is important to note that SCHENCK (*vide* PALMER 1915) as early as 1904 indicated that the pigment of the yolk of the egg and of the blood serum of the hen is identical with one of the forms of xanthophyll,—L-xanthophyll,—which he had isolated from plant tissue. More recent work by WILLSTÄTTER and ESCHER (*vide* PALMER 1915), who have isolated the pigment from the yolks of 6000 hen's eggs, leads them to the conclusion that the principal coloring material of the fowl's egg is isomeric with the crystalline xanthophyll of the chloroplast. PALMER (1915) from his chemical and feeding studies holds that xanthophyll is the principal natural pigment of the egg yolk, body fat and blood serum of the hen, just as he and one of his associates (ECKLES) earlier showed that carotin is the natural pigment in the corpus luteum, body fat, blood serum and milk fat of the cow.

The chief interest of these studies in the present connection is that they indicate *the identity of body and yolk pigment*, thus supporting the view that the correlations here demonstrated rest primarily upon physiological phenomena of the migration of fat-soluble yellow pigment.

The best source of information concerning the mechanism of pigment redistribution is work on feeding of Sudan III and other substances capable of staining fat in the living organism initiated in the investigation of the physiology of the bird by RIDDLE (1907, 1908, 1910, 1911) and continued by GAGE and GAGE (1908), MENDEL and DANIELS (1912), ROGERS (1912) and others. Those who are interested in the details of this subject from the standpoint of the physiological chemist must turn

to the original papers. For the purposes of the present paper it is sufficient to point out that in the later rapidly developing stages of the yolk of the fowl's egg Sudan III will be taken up from the alimentary canal in large quantities. Indeed, RIDDLE has shown that, with heavy feeding, perceptible amounts of the stain will appear in the egg at the end of two or three hours. As the studies of GAGE and GAGE (1908) and others have shown, the Sudan III may be transferred from the yolk fat to that of the young chick.

The generalization to be drawn from the many varied experiments with Sudan III is that while in the animal body it clings at all times to the fats or their constituent fatty acids, and so goes quite mechanically wherever these particles go. This does not, however, preclude the possibilities of differential distribution of the pigment throughout the body. Nor does it preclude the possibility that the fat of the egg may withdraw pigment from the fat of the body tissues.⁷ The ovum of the fowl has not merely the capacity of taking up the fat (and with it the Sudan III stain) from recently injected food, but of developing at the expense of body (stored) fat as well.

For the purposes of the present discussion nothing need be said concerning the manner in which either the fat or the fat-soluble pigment which goes along with it, is carried in the blood, or concerning the mechanism of its distribution throughout the body, or of its translocation from body tissues to the yolk. For all such data, which are as yet far from complete, the reader must consult the original physiological literature.

RECAPITULATION

The present paper is a contribution to the general problem of the relationship between somatic characters and fecundity. Specifically it presents and analyzes by means of the modern higher statistics, data bearing upon the relationship between the concentration of yellow pigment in the ear lobe of White Leghorn hens and their egg records of the preceding months.

The data comprise pigmentation evaluations and egg records for 309 and 375 birds entered in the 1913-'14 and 1914-'15 International Egg-Laying Contest held at Storrs, Connecticut.

⁷ A quite analogous case of the withdrawal of the pigment from the tissues by the developing egg is furnished by the natural pigment of the egg of salmon. It is practically certain that here the natural coloring matter is derived from the muscles of the fish, from which the fat in which most if not all the coloring matter resides, is transferred to the ovary and to the growing eggs.

The egg records cover a period of one year, November to October, inclusive, of the pullet year. Pigmentation determinations were made in October, that is at the close of the laying period considered. The measures of yellow pigment concentration were obtained by the use of the white and yellow sectors of the color top. The ear lobe was selected for measurement because it presented the least practical difficulty in the quantitative measurement of pigmentation. The results here presented will be confirmed by more qualitative determinations made for these and other birds on the leg, beak and vent.

Incidental to the discussion of the main problem, considerable series of constants for mean fecundity and for variation and correlation in fecundity in the White Leghorn are given. For these the reader must refer to discussions in the body of the paper. With regard to the central problem, the statistical analysis of the data leads to the following conclusions:

There is a very close interdependence between October ear lobe color and the egg production of the year. Numerically the correlation, measured on the universally applicable scale of -1 to $+1$, is expressed by a constant of the order $r = -.550$. The negative sign indicates that *higher* concentrations of yellow pigment are associated with *lower* annual egg record. The results for the two years are in close agreement.

Expressed in absolute instead of relative terms, the correlations determined indicate that on an average birds differing by 5 percent in the amount of yellow in the ear lobe will differ by about 7 eggs in their annual production. Thus the difference is one of very real practical significance. For example, birds showing only 10-20 percent of yellow in their ear lobes in October will have laid on an average about 185 eggs each, whereas, birds exhibiting 55-65 percent of yellow will have an average annual production of only about 130 eggs.

The correlations between October pigmentation and the egg production of each month of the year have also been determined for the two years. All of these coefficients are negative in sign. Thus they show that a high percentage of yellow in October indicates lower egg production not merely in the year as a whole, but in each individual month of the year as well. Almost without exception these coefficients may be considered significant in comparison with their probable errors. The results for the individual months are in remarkably good agreement in the two years. In not a single case can the differences between the constants for the same month in the two competitions for which data are

available be considered greater than those to be attributed to experimental errors.

While all the correlations between October pigmentation and the egg production of the individual months are negative in sign, they differ greatly in magnitude. Beginning with a correlation of about $-.150$ in November, the intensity of the relationship increases numerically to about $-.250$ in December, after which it falls to practically zero in March and April, and then increases in (negative) intensity rapidly to about $-.750$ in October.

The fact that roughly speaking the correlation increases in intensity as the two variables become more closely associated in time, suggests that the correlation demonstrated is of a purely physiological nature. The hypothesis that the growth of the egg abstracts certain substances—in the present case, yellow pigment—from the body tissue, or precludes its being deposited there, would at once account for the generally higher correlation between measures made at more closely associated periods of time.

If this view be the correct one, egg production must be regarded as the (relatively) independent variable, and intensity of pigmentation as the dependent variable. Egg production would then be looked upon as the chief proximate cause of the observed intensity of pigmentation.

For a detailed discussion of a number of lines of evidence for this view, the reader must consult preceding pages.

The fact that pigmentation has throughout this paper apparently been taken as the more fundamental character must not suggest that it has ever been considered by the authors to be such *physiologically*. Any such emphasis results merely from the fact that we have been seeking to determine the prediction value of a somatic character for use in the selection of birds characterized by high egg production without actually determining their record by trap-nesting.

Finally those who may be interested in the practical application of the results here secured must bear in mind the fact that the flocks from which our data were obtained represent a selected class of birds. Only groups of birds which are supposed to be the most promising are placed in the competition. The birds in the contest show, because of better breeding, better feeding and care, or both, a far higher annual egg production than those of the average flock. Unfortunately data of the kind presented here are not as yet available for the unselected class of layers.

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THE PROBABLE ERROR OF A DIFFERENCE AND THE SELECTION PROBLEM¹

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IN GENETICS for July, 1916, appears an interesting and suggestive paper by ACKERT (1916) on the effect of selection in *Paramecium*. The general logical method of this paper, with its insistence on the statistical presentation of adequate quantitative evidence, is altogether praiseworthy. And furthermore there will be little doubt in the mind of anyone who has followed recent genetic literature at all closely that the general conclusion reached is of a sort to be entirely satisfactory to the present writer. I cannot, however, permit a gross error in a particular biometric method, largely made use of in ACKERT's paper, to pass without protest, because it seems to me to make the author's otherwise satisfactory general conclusion that selection is without effect, rest upon an extremely insecure statistical foundation.

At various places in his paper (pp. 390, 395, 402) ACKERT makes statements about probable errors of differences between means, calculated on the basis that the probable error of a difference is the sum of the probable errors of the quantities entering into the difference. Such is not the fact. It has long been known that the standard deviation of a difference between two constants is given by the following expression (cf. PEARL 1909).

Let $z = x - y$.

$$\text{Then } \sigma_z = \sqrt{(\sigma_x^2 + \sigma_y^2 - 2r_{xy}\sigma_x\sigma_y)} \quad \text{----- (i),}$$

where x and y denote any statistical constants, and z the difference between them. Also σ denotes the standard deviation of the variable indicated by its subscript, and r_{xy} is the coefficient of correlation between x and y . Now in ordinary cases of statistical comparisons, the constants compared are derived from distinct and separate samples, so that r_{xy} necessarily equals 0.² Equation (i) then becomes, of course,

$$\sigma_z = \sqrt{\sigma_x^2 + \sigma_y^2} \quad \text{----- (ii),}$$

¹ Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 103.

² One should never assume without careful consideration, however, that $r_{xy} = 0$ in any particular case. The possibilities in the way of unsuspected error correlations are large.

which, remembering that in a distribution of unit area the "probable error" is 0.6744898..... times the standard deviation, leads to the usual rule of statistical texts that "the probable error of a difference is equal to the square root of the sum of the squares of the quantities entering into the difference." ACKERT has apparently tried to simplify this rule still further by assuming that the square root of the sum of the squares of two quantities is the same as the sum of the quantities. Unfortunately it is not.

Now suppose we calculate correctly the probable errors of the differences in ACKERT's table 8 (p. 402) and see how the results then appear. Table 1 is a reconstruction of ACKERT's table 8, with the addition of (a) the probable errors of the differences, and (b) the quotient diff./P.E. diff. , and (c) recalculated and corrected values of the probable errors of the means themselves. In only one case out of all the probable errors in ACKERT's table 8 was the probable error of a mean as printed found upon recalculation to be entirely correct. In most cases the errors concerned only the third place of figures, and evidently arose from the fact that he did not carry sufficient places of decimals in his intermediate calculations to give a correct value for the final place in the tabled results. In a few cases, as will be seen by comparison of table 1, with ACKERT's table 8, the probable errors of the means are grossly incorrect, due probably to some large undiscovered slip in the arithmetic. Of course in making the recalculations his values of the standard deviations had to be used, since he gives no frequency distributions from which they may be independently calculated, but only diagrams, too coarse to read accurate integral frequencies from. So then the values of the probable errors given in table 1 are correct to 3 places of decimals, on the assumption that ACKERT's standard deviations are correct to the same degree.³

From this enlarged table we note the following points:

1. In three out of the four experiments (viz., 2, 3 and 4) the progeny

³ It is a disagreeable task to call attention to small arithmetical errors, but much American biometrical work is fearfully and wonderfully weak in its elementary arithmetic. If one tables constants to 3 places (or any other number of places) of decimals the presumption is that the results are *accurate as far as tabled*. Mathematicians follow such a code. If biologists are going to use mathematical methods they must eventually do the same thing. But how many biologists are there who even *know* how many places of decimals must be carried in intermediate computations to ensure that the second, third, fourth, or *n*th place in the final result shall be correct?

TABLE I

ACKERT'S results on *Paramecium*.

Length in microns					
	Group	Parents	Offspring	Difference	Diff./P.E. diff.
Group A Experiment 1	A ₁	90	124.996 \pm 0.283	0.650 \pm 0.414	1.57
	A ₂	162	124.346 \pm 0.302		
Group B Experiment 2	B ₁	162	179.540 \pm 0.466	4.778 \pm 0.618	7.73
	B ₂	235	174.762 \pm 0.406		
Group C Experiment 3	C ₁	162	167.105 \pm 0.479	3.071 \pm 0.692	4.44
	C ₂	198	164.034 \pm 0.500		
Group D Experiment 4	D ₁	135	125.307 \pm 0.356	7.311 \pm 0.504	14.51
	D ₂	184	117.996 \pm 0.357		

Breadth in microns					
	Group	Parents	Offspring	Difference	Diff./P.E. diff.
Group A Experiment 1	A ₁	36	55.050 \pm 0.144	0.760 \pm 0.209	3.64
	A ₂	45	54.290 \pm 0.152		
Group B Experiment 2	B ₁	45	56.359 \pm 0.200	1.281 \pm 0.262	4.89
	B ₂	54	57.640 \pm 0.170		
Group C Experiment 3	C ₁	36	66.093 \pm 0.185	1.707 \pm 0.297	5.75
	C ₂	45	67.800 \pm 0.232		
Group D Experiment 4	D ₁	60	44.923 \pm 0.200	3.288 \pm 0.309	10.64
	D ₂	64	48.211 \pm 0.235		

population from the *shorter* selected parent is *significantly longer* than the population from the originally longer parent. The differences are so great in comparison with their probable errors in every one of these cases as to make the odds from 332 to 1 (in the case of experiment 3) to far above 1,000,000,000,000 to 1 (in the case of experiment 4) against their being accidental or due to random sampling (cf. PEARL and MINER 1914). Now in order to prove that selection was without effect the

means in the two compared groups in each case should be *the same*, within the limit of errors due to sampling. How far the facts are from such a condition is sufficiently evident from the above figures.

2. In the same three experiments (2, 3 and 4) the progeny population from the *broader* parent is significantly *broader* than the population from the narrower parent. The differences are so large in comparison with their probable errors that the odds against their being accidental range from about 1052 to 1, in experiment 2, to a magnitude which is far beyond human conception in experiment 4.⁴

3. Experiment 1 gave a result totally unconformable, when mathematically considered, with the other experiments. Here there is no significant difference in the mean lengths. The breadth means differ by a probably significant amount in the opposite direction to that in which the selection was made.

It is of course impossible for the present writer to hazard any opinion as to the cause of the statistically enormous differences which appear in ACKERT's experiments. He suggests (p. 395) that they may be "due to an uncontrolled factor in the environment." Probably this is true, but if it is, just what bearing on the selection problem do the results have? It seems very clear that if, in an experiment designed to test the effect of selection, there are environmental differences acting upon compared groups, so great that they cause differences of the relative magnitude exhibited in ACKERT's data, the results can by no possibility have any critical worth whatever in the discussion of the selection problem. They leave that problem in precisely the same status that it was before. This would seem to be exactly the fact in regard to the effect of selection in *Paramecium*. The work of JENNINGS (1908) demonstrated, so far at least as the strains with which he worked are concerned, that selection for size differences within the pure line in *Paramecium* is without effect. ACKERT's work neither confirms nor refutes that result.

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⁴The odds against a deviation 8 times the probable error are 1,470,588,234 to 1. Here we have a deviation 10.6 times the probable error!

CROSSING OVER OHNE CHIASMATYPIC?

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I

Es ist wohl nicht zu viel gesagt, wenn man behauptet, dass MORGANS und seiner Mitarbeiter Untersuchungen an *Drosophila* die wichtigste Bereicherung der Vererbungslehre in den letzten Jahren darstellt. Sie sind ein Musterbeispiel für ein zielbewusstes Handinhandarbeiten von Vererbungsexperiment und cytologischer Forschung und ihre Hauptergebnisse gehören jetzt schon zum wichtigsten Schatz unserer Wissenschaft. Wenn irgendwelche Arbeiten im Stande waren, auch die letzten Zweifler von der Richtigkeit der Chromosomenlehre der Mendelschen Vererbung zu überzeugen, so sind es diese. Diese Ueberzeugung soll uns aber nicht blind machen und verhindern, da Kritik anzulegen, wo es notwendig erscheint. Wenn dies im Folgenden geschehen soll, so tue ich es in der Ueberzeugung, dass die Tragweite der MORGANSchen Resultate nur erhöht werden kann, wenn sie von Folgeschlüssen befreit sind, die nicht notwendig sind, und so bestechend und geistreich sie auch sein mögen, einer weiteren Vertiefung der Erkenntnis dadurch schaden, dass sie sie in einer bestimmten, aber nicht notwendigen Richtung festlegen.

Der auffallendste und imposanteste Schluss aus MORGANS Arbeiten ist natürlich der, dass er aus den Zahlenverhältnissen der "crossover" Klassen in den Zuchten auf die relative Lage der körperlichen Äquivalente der Erbfaktoren im Chromosom schliessen kann. Und dieser Schluss wieder basiert auf der Annahme, dass der in seinen Zahlenverhältnissen typische Austausch zwischen den homologen Chromosomen durch den Austausch von Chromosomensegmenten im Gefolge einer Chiasmotypie gegeben wird. MORGAN selbst ist sich natürlich der Tatsache bewusst, dass die Annahme von JANSSENS Theorie der Chiasmotypie, so weit die cytologischen Tatsachen in Betracht kommen, ziemlich in der Luft schwebt. Man könnte ihm trotzdem in der Verwendung dieser Hypothese, angesichts ihres Erklärungswerts, zustimmen, wenn sie nötig wäre. Aber das ist nicht der Fall. Und nicht nur dies, es erscheint uns sogar, dass die Chiasmatypiehypothese und die sich daraus ergebenden

den Konsequenzen in bezug auf die Lagerung der Faktoren im Chromosom ein Nachteil ist. Sie legt unsere Vorstellungen auf einen relativ einfach erscheinenden, grobsinnlichen Vorgang fest und belastet uns damit mit einer Kette, die unter Umständen verhindert, dass aus den gleichen Tatsachen noch weiterreichende Schlüsse gezogen werden können. Sie täuscht uns die Erreichung einer zweiten Stufe der Erkenntnis vor, während in Wirklichkeit nur die erste erreicht ist, und aus den zahllosen gleichberechtigten Möglichkeiten für die zweite, nur eine einzige, leicht sinnlich vorstellbare, heraus gegriffen ist. Es wird sogleich klar werden, was wir damit meinen.

Die erste Stufe, die unseres Erachtens durch MORGANS Experimente mit Sicherheit erreicht ist, ist der Nachweis, dass Faktoren zwischen den Chromosomen eines Paares ausgetauscht werden können und dass das Mass, in dem sie ausgetauscht werden, für je zwei oder mehr gegebene Faktoren unter gleichen äusseren Bedingungen ein typisches ist, variierend zwischen vollständiger "Linkage" oder Nichtaustausch und freier Spaltung oder beliebigem Austausch. Die zweite Stufe der Erkenntnis wäre dann der Nachweis der Kräfte, die dies quantitativ verschiedenartige Verhältnis des Austausches bedingen. Für MORGAN ist es die Chiasmotypie und die Entfernung der Faktoren im Chromosom, also morphologische Lagebeziehungen, die dafür verantwortlich sind. Dies ist der Schluss, den wir als unnötig nachweisen wollen, indem wir zeigen, dass für die Erklärung jener quantitativen Verhältnisse die gleichen Kräfte ausreichen, die überhaupt beim Aufbau eines Chromosoms aus Faktoren am Werk sein müssen, welcher Art sie auch seien. An die Stelle jener Schlussfolgerung wollen wir eine viel allgemeinere setzen, von der MORGANS Hypothese nur ein grobsinnlich gefasster Spezialfall ist. Er sieht in den unbekannten, quantitativ bestimmten Kräften des Austauschs eine entsprechende Entfernung der Faktoren im Chromosom. Es ist aber doch klar, dass man jede Proportion geometrisch als Entfernungen auf einer Geraden darstellen kann. Wenn diese Darstellung also im gegebenen Fall stets mit den Tatsachen übereinstimmt, so beweist das nicht etwa, dass nun wirklich Entfernungen auf einer Geraden hinter der Erscheinung als Ursache stehen, sondern es beweist nur, dass irgendwelche Kräfte im Spiel sind, deren relativer Effekt als Entfernungen auf einer Geraden dargestellt werden können. Wir glauben, dass es sehr wichtig ist, dies uns klar zu machen; denn während MORGANS Hypothese nur den allereinfachsten denkbaren Spezialfall in

Betracht zieht, erlaubt jene allgemeine Fassung nicht nur alle möglichen anderen Vorstellungen, sondern lässt auch die wichtige Möglichkeit zu, später einmal aus den beobachteten Zahlenverhältnissen Schlüsse auf die wirkliche Art der wirkenden Kräfte ziehen zu können, ähnlich wie man aus den bei Temperatur- und Variationsversuchen an Embryonen gewonnenen Zahlen auf den chemischen Charakter der zu Grunde liegenden Reaktionen schliessen konnte. Wir wollen somit beweisen—was eigentlich auch ohne besonderen Beweis klar sein sollte—dass aus den Crossover-Experimenten nur dies folgt, dass das Mass des Crossing over der Ausdruck irgendeiner quantitativ variablen Kräfte wirkung ist, die für die Zugehörigkeit eines Determinanten zu einem der Chromosomenpartner verantwortlich ist, eine Kraft deren relative zahlenmässige Wirkungen natürlich auch geometrisch als Abschnitte einer Geraden dargestellt werden können.

II

MORGANS Schlussfolgerungen aus seinen Versuchen, und zwar sowohl die, die uns hier beschäftigen, wie alle anderen cytologischer Natur, basieren auf einer Reihe von Annahmen, die ein jeder Anhänger der Chromosomenlehre der Vererbung machen muss. Ueber sie wollen wir uns zuerst einmal klar werden. Da ist zunächst die Annahme der Individualität der Chromosomen, ohne die ja überhaupt eine Parallele zwischen Chromosomenverteilung und Faktorensplaltung nicht durchführbar ist. Sodann haben wir die Annahme, dass in jedem Chromosom mehrere und verschiedenartige Erbfaktoren enthalten sind. Für ihre Richtigkeit bringen ja gerade MORGANS Untersuchungen so überzeugendes Beweismaterial bei. Sodann muss angenommen werden, dass die Lagerung der Teilchen, die den Erbfaktoren entsprechen, innerhalb des Chromosoms eine typische ist, ob wir sie uns nun linear angeordnet vorstellen oder nicht. Denn sonst wäre ein geordnetes "Crossing over" überhaupt nicht denkbar. Daraus folgt aber noch eine andere wichtige Annahme. Während der Kernruhe werden die Chromosomen körperlich desintegriert. Bei der nächsten Teilung finden sie sich aber wieder unter Wahrung der Individualität vor. Es müssen also irgend welche Kräfte im Spiel sein, die bei der Bildung der Chromosomen immer wieder jedem Partikelchen-Erbfaktor seinen Platz im richtigen Chromosom und am richtigen Platz

anweisen. Ob dies nun für gewöhnlich ausgesprochen wird oder nicht, sicher ist, dass jede Chromosomenhypothese auf dieser Vorstellung basiert.

Und nun bleiben wir einmal bei diesem letzteren Punkt. Da ist es zunächst klar, dass wir über die Art der Kräfte, die die richtige Sammlung der Partikelchen zum Chromosom bedingen, nichts wissen. Es mögen chemische Affinitäten sein, es mögen Wirkungen der Massenkraft sein, es mögen grobmechanische Dinge sein. Aber unter allen Umständen müssen sie spezifisch und typisch für jedes gegebene Partikelchen-Erbfaktor sein. Ist dies schon für irgend eine geordnete Lagerung der Teilchen im Chromosom nötig, so ist es gewiss so für eine geordnete lineare Lagerung, mit der auch Morgan arbeitet. Für unsre weiteren Auseinandersetzungen ist es gänzlich gleichgültig, wie wir uns die typische, geordnete Lagerung vorstellen. Und so ist es das Einfachste, dass wir uns auch die Dinge als lineare Anordnung der Partikelchen versinnlichen, da es die einfachste graphische Darstellung erlaubt; auch der Chemiker benutzt ja flächenhaft angeordnete Symbole anstatt der verwickelteren stereometrischen Vorstellung, ohne sie deshalb als eine Realität zu nehmen. Wenn nun also die Partikelchen sich zu einer typischen Reihe spezifischer Anordnung immer wieder zusammenfinden sollen, so müssen, wie gesagt, die wirkenden Kräfte für jedes einzelne in Bezug auf seine Nachbarschaft typisch sein. Wenn wir uns das versinnbildlichen wollen, so können wir die Kräfte, die einem Partikel die Lage neben einem andern und nur neben diesem anweist, als eine Wirkung bestimmter Quantität darstellen und graphisch könnten wir uns dann die Festlegung eines bestimmten Platzes im Chromosom für ein Partikelchen so veranschaulichen wie es Fig. 1 wiedergibt. Die Kraft, die ein Partikelchen-Erbfaktor an sein Chromosom kettet ist durch einen rechteckigen Anker wiedergegeben, dessen Grösse der Quantität dieser Kraft entspricht. (Wir "verankern" den Faktor an seinem Chromosom im Interesse der graphischen Darstellung; sachlich kann das aber eben so gut die Verankerung an seinem Nachbar oder sonst etwas bedeuten). In der Figur 1 sind somit die Erbfaktoren *ABCD* enthalten, die ihre richtige Lagerung in dem betreffenden Chromosom—die hier linear dargestellt ist aber ebenso gut irgend eine stereometrische Form haben könnte—den spezifischen Kräften von der spezifischen Quantität und Qualität *w x y z* verdanken. Wenn wir nun das entsprechende Chromosom einer Form darzustellen hätten, die an Stelle von *B* nur *b* enthält, so könnten wir es entweder unter wörtlicher Auslegung der presence-

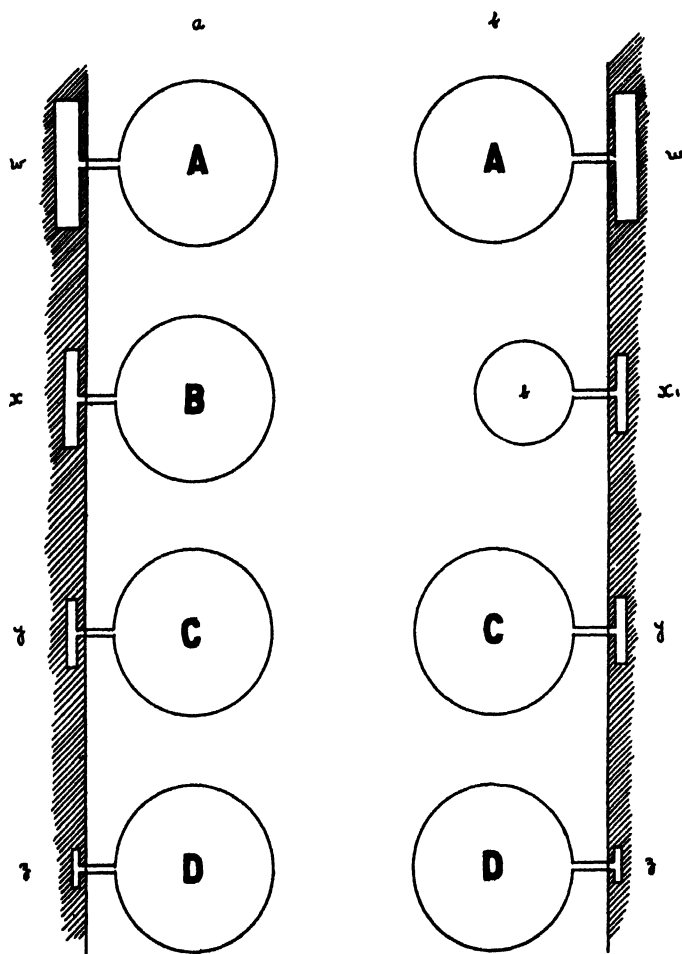


FIG. 1

absence Theorie so machen, dass hier *B* fehlt, oder auch einen andersartigen Faktor *b* einfügen, dessen Andersartigkeit sich auch in seiner andersartigen und spezifischen Verankerung zeigt also x_1 statt x . Sachlich ist es gleichgültig, welche Darstellung wir wählen, denn schliesslich sind ja beide nur differente Anschauungsformen von presence-absence. Die letztere ist bequemer zu handhaben und daher in Fig. 1 *b* angewandt. Wenn wir nun den Bastard *Bb* vor uns haben, so werden also auch bei ihm bei der Chromosomenbildung die Faktoren *B* und *b* an ihren richtigen Platz in dem richtigen väterlichen oder mütterlichen Chromosom sich einfinden und Fig. 1 wäre dann eine Darstellung eines Chromosomenpaares dieses Bastards. Wie schon gesagt, hier haben wir

nicht das geringste Neue ausgesagt, sondern einfach die selbstverständlichen Voraussetzungen der Chromosomenlehre uns graphisch klar gemacht.

Daraus folgt nun ohne Weiteres das Folgende: Sind die Kräfte x und x_1 quantitativ so verschieden, dass sie nicht vertauscht werden können, so können die Faktoren B und b stets nur wieder sich in ihrem ursprünglichen Chromosom einfinden; im Vererbungsversuch erschienen sie also vollständig "linked" mit dem Rest der Faktoren. Wären die Kräfte x , x_1 aber so ähnlich, dass sie vollständig freien Austausch der Faktoren gestatteten, die sich somit beliebig in jedem der beiden elterlichen Chromosomen an dem betreffenden Platz einfinden könnten, so müssten Bb eine reine Mendelspaltung zeigen, die nicht von einer Spaltung von in differenten Chromosomen gelagerten Faktoren zu unterscheiden wäre. Wären endlich aber die Kräfte x , x_1 variabel und ein Überschneiden der Curven fände statt, so hätten nur die in dem gemeinsamen Kurvenbezirke gelegenen Fälle die Möglichkeit ihren Platz in dem einen oder anderen Chromosom zu finden, d.h., zu cross over. Diese drei Möglichkeiten können wir uns an den nebenstehenden Variationskurven für die Kräfte x , x_1 ohne Weiteres klar machen (Fig. 2),

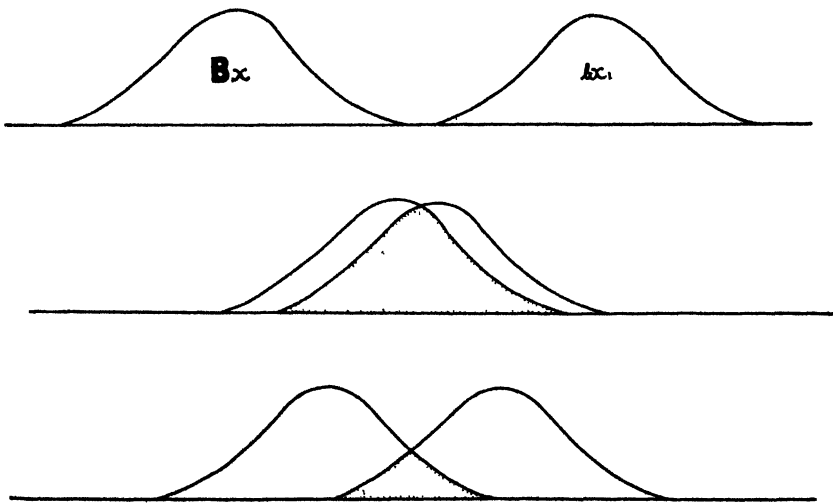


FIG. 2

wobei natürlich die einfachste Annahme über die Art der Variation gemacht ist. Die Zahl der Fälle des Hinüberkreuzens eines Faktors wäre aber proportional der Grösse des gemeinsamen Kurvenbezirks, und bei

zwei Faktoren, die allein ja das Resultat erkennen liessen, proportional der Combination beider Kurvenbezirke. Und wenn, wie selbstverständlich, die Werte x , x_1 , etc., zu den typischen Qualitäten der Faktoren B , etc., gehören, so muss auch in diesem Fall für jede Faktorenkombination der Prozentsatz des Hinüberkreuzens unter gleichen Bedingungen konstant sein. So zeigt es sich, dass die ganze Erscheinung des Crossing over eine logische Konsequenz aus der Individualität der Chromosomen ist, somit keine weitere Hilfhypothese zu ihrer Erklärung nötig ist. Es zeigt ferner, dass der typische Prozentsatz der crossover Klassen ganz allgemein der Ausdruck einer entsprechend typischen Verschiedenheit der Chromosomenaufbau aus den Einzelfaktoren bedingenden Kräfte ist; und somit gar kein Bedürfnis vorliegt, an Stelle der Kräfte relationen, deren Wirkung natürlich auch geometrisch als Abschnitte einer Geraden dargestellt werden können, die ganz bestimmte Vorstellung der Chiasmatype und räumlichen Entfernung zu setzen.

Hier könnte nun noch die Frage aufgeworfen werden, ob ein derartiger Faktorenaustausch nicht eben so gut in den diploiden Keimbahnzellen stattfinden müsse, wie in den Geschlechtszellen vor den Reifeteilungen. *A priori* lässt sich dies in der Tat nicht leugnen. Sachlich würde das aber nichts ändern, sondern nur bedeuten, dass das Mass des Crossover eine Funktion von zwei Variablen, nämlich sowohl der betreffenden Verankerungskräfte als auch der Zahl der somatischen Keimbahnteilungen ist. In Fällen, in denen die Crossoverzahlen in verschiedenen Versuchen verschieden ausfallen (etwa bei *Antirrhinum*) mag tatsächlich diese Annahme die Erklärung liefern. Sonst ist sie unnötig und daher empfehlenswert nur mit einem einmaligen Austausch in der Synapsis und Wachstumsperiode zu rechnen.

Als wichtig erscheint in diesem Zusammenhang auch das folgende. Es ist bemerkenswert, dass bei *Drosophila* der Faktorenaustausch nur im weiblichen Geschlecht stattfindet, in anderen Beispielen nur im männlichen oder in beiden. Wenn der Austausch bedingt wird durch die transgredierende Variation zweier Kräfte, so sollte diese abhängig sein von Aussenfaktoren. Die Aussenwelt für die Chromosomen ist zunächst der Kern. Tatsächlich gehen während der den Reifeteilungen vorausgehenden Wachstumsperiode im Keimbläschen Umwälzungen vor sich,

die die Variationsursachen abgeben könnten. Das Crossing over fände dann bei dem Neuaufbau der Chromosomen zu den Reifeteilungen statt, und eventuelle Verschiedenheiten darin zwischen den Geschlechtern wären zu erklären aus den Bedingungen dieser Periode, die Variation begünstigen oder nicht. Damit stimmt auch die Tatsache überein, dass die Crossoverzahlen durch äussere und innere Einflüsse (Altern bei *Drosophila*) verändert werden können. Dies ist natürlich auch nur eine Hypothese, die für die Gesamtbetrachtung nicht wesentlich ist.

Um Missverständnisse zu vermeiden sei an dieser Stelle nochmals folgendes hervorgehoben. Es ist nicht meine Absicht, an Stelle von MORGANS Hypothese eine andere zu setzen, oder gar seine Darstellung als grobsinnliches Schema zu verwerfen, und dann durch Aufstellung eines anderen Schemas denselben Fehler zu begehen. Das, was ich beweisen will, ist vielmehr, dass die Tatsachen auf Grund der von jedermann anerkannten Voraussetzungen der Chromosomenlehre verstanden werden können; dass dieselben Kräfte, die die Chromosomenindividualität bedingen, auch für die Erklärung des Crossing over ausreichen; ferner, dass wir für die Wirkung dieser unbekannten Kräfte verschiedene diagrammatische Darstellungen wählen können, die der graphische Ausdruck von Zahlenrelationen sind; und sodann, dass wir eine passende graphische Darstellung nicht mit der Wirklichkeit verwechseln sollen, da wir uns dadurch den Weg für weitere Erkenntnis versperren, besonders für eine solche physikalisch-chemischer oder dynamischer Natur.

III

Die hier entwickelten Anschauungen sind von mir schon mehrfach, für den Fachmann verständlich, angedeutet worden. JANSSENS Chiasmotypie-Theorie sollte ja eine Erklärung für die Möglichkeit des Vorhandenseins mehrerer spaltender Faktoren in einem Chromosom geben. Die crossover Theorie steht aber auf der gleichen Basis. Schon 1911 habe ich eine Idee entwickelt, wie das Vorhandensein mehrerer selbstständig spaltender Faktoren in einem Chromosom erklärt werden kann, der prinzipiell derselbe Gedankengang, wie der hier durchgeführte, zu Grunde liegt. Die damaligen Ausführungen hatten aber den Nachteil, dass sie mit der Annahme der end-to-end Conjugation verquickt waren und auch mit einer zu wörtlichen Auslegung der presence-absence Theorie. Sie haben daher auch keine weitere Beachtung gefunden.

Diese früheren Äusserungen haben wohl MORGAN, MULLER, STURTEVANT u. BRIDGES (1915) im Sinn, wenn sie von der Anschauung "einer

Anzahl Genetiker" sprechen,¹ die das Crossover mit dem Chromosomenaufbau aus Partikelchen in Zusammenhang bringen. MULLER (1916) geht in seiner neuesten Arbeit etwas näher auf diesen Punkt ein. Da im Vorhergehenden und Folgenden alle von ihm angeführten Punkte ohnehin besprochen werden, brauchen wir hier nicht noch einmal darauf zurück zu kommen. Aber es erscheint doch wünschenswert, noch im Speziellen zu zeigen, dass tatsächlich die Versuchsergebnisse in der hier durchgeführten Weise erklärt werden können.

Nehmen wir an, wir hätten in einem Versuch zu tun mit den elterlichen Faktoren AB und ab . Bei dem Aufbau der Chromosomen zur Reifeteilung gelangen also normaler Weise AB und ab in die homologen Chromosomen. Wenn die Kraft, die ihnen ihren Platz anweist bei A und a oder B und b sehr verschieden ist, tritt völlige "Linkage" ein. Ist sie aber nur soweit verschieden, dass die Grenzfälle transgredieren, dann tritt Crossing over ein. Nehmen wir nun an, dass für die Faktoren Aa die elterliche Lage im Chromosom 3 mal so oft eintritt als das Ueberkreuzen, also unter 4 Fällen 3 normal sind; ferner, dass für die Faktoren Bb das gleiche Verhältnis 5 : 1 sei. Dann wird, falls dies nur in einem Geschlecht stattfindet, das Verhältnis der elterlichen Kombinationen zu den crossover Klassen Ab und aB gleich 16 : 8 sein oder 50 Prozent. Wenn wir anstatt 3 : 1 und 5 : 1 allgemein setzen $p_a : 1$ und $p_b : 1$, so giebt uns

die Formel
$$\frac{100 (p_a + p_b)}{(p_a + 1) (p_b + 1)} = cr$$
 die crossover Klassen für $AaBb$ in

Prozent wieder. Empirisch gefundene Werte für cr könnten natürlich auf sehr verschiedenen Werten von p_a und p_b beruhen. Wenn aber noch ein drittes Faktorenpaar Cc hinzu kommt, so legen die crossover Prozente für AB , AC und BC die Werte p_a p_b p_c fest. Nehmen wir nun einmal eine Serie von Faktorenpaaren Aa Bb Cc Dd , etc., und setzen für sie angenommene Werte für p_a , p_b . . ., nämlich:

$$p_a = 3$$

$$p_b = 4$$

$$p_c = 10$$

$$p_d = 20$$

$$p_e = 50$$

$$p_f = 1000$$

und rechnen die danach zu erwartenden crossover Prozente für die verschiedenen Faktorenkombinationen aus, dann sind

¹ Auch STOMPS (1912) hat einmal ähnliche Äusserungen veröffentlicht.

$cr AB = 35.0\%$ $cr BC = 25.5\%$ $cr CD = 13.0\%$ $cr DF = 6.5\%$
 $cr AC = 29.5\%$ $cr BD = 22.9\%$ $cr CF = 10.7\%$ $cr DI = 4.9\%$
 $cr AD = 27.4\%$ $cr BF = 21.2\%$ $cr CI = 9.9\%$ $cr FI = 2.1\%$
 $cr AF = 26.0\%$ $cr BI = 20.1\%$
 $cr AI = 25.0\%$

Wenn wir dann diese Werte graphisch nach MORGANS Vorgang als Distanzen auf einer Geraden darstellen und dabei, wie MORGAN es tut, die kürzesten Strecken als massgebend nehmen, erhalten wir:

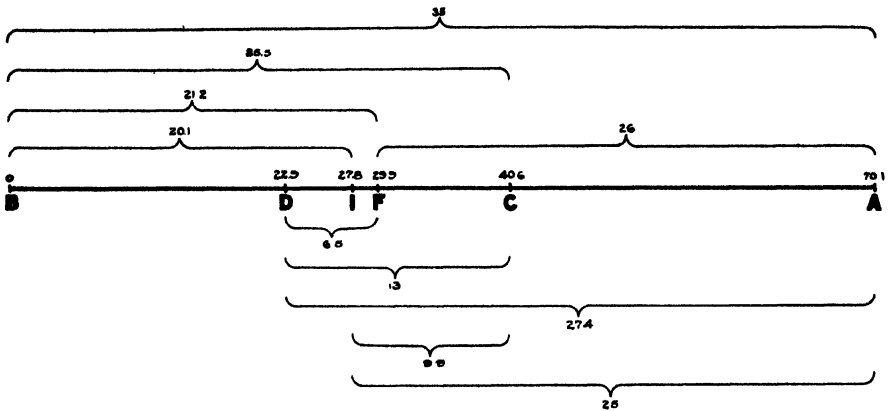


FIG. 3

Stellen wir nun daneben ein analoges Schema nach STURTEVANTS (1913) Untersuchungen über die *Drosophila*-Faktoren *B*, *CO*, *P*, *R*, *M*:

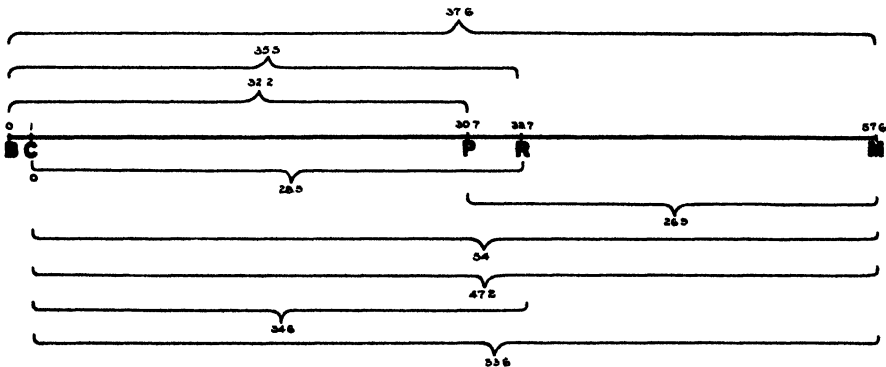


FIG. 4

Dies letztere soll die folgenden Gesetzmässigkeiten zeigen: Wenn es sich um kleine Distanzen handelt, giebt die Addition zweier Teilstrecken ziemlich genau den für die ganze Strecke berechneten Wert, z.B., $BP=32.2$, $PR=3$ und $BR=35.5$. Analog wäre in unserem Schema

$BI=20.1$, $IF=2.1$, $BF=21.2$; $AI=25.0$, $ID=4.9$, $AD=27.4$. Wenn es sich um grössere Distanzen handelt, giebt die Addition der Teilstrecken eine grössere Summe als die Berechnung des Gesamtdistanz, z.B., B , CO , P , R , $M=57.6$, $BM=37.6$, oder CO , P , $M=56.6$, $COM=54$ resp. 33.6 resp. 47.2 . Dem steht gegenüber im ersten Schema $B D I F C A=70.1$, $BA=35.0$; oder $B D I F C=40.6$, $BC=25.5$. Daneben finden sich aber noch allerlei nicht besonders hervorgehobene Inkongruenzen, z.B., bei STURTEVANT $CR=28.5$, $CP=30$, also eine Summe kleiner als eines der Teilstücke. Ebenso $CM=33.6$ aber $CR=34.6$. Bei uns entspricht dem $BD=22.9$, $BI=20.1$. Da $DI=4.9$ so würden wir, wenn nur diese 3 Werte bekannt wären, I zwischen B und D setzen und es stimmte dann. Das Gleiche wäre aber der Fall, wenn STURTEVANT nur die drei obigen Zahlen hätte. Ferner zeigt es sich, dass man verschiedene Werte für die gleiche Strecke bekommt bei verschiedener Art der Berechnung. So bei STURTEVANT für BM aus $BC+CP+PR+RM=57.6$; aus $BR+RM=59.4$; aus $BO+OM=48.4$; aus $BC+CM=34.8$, etc. Dem entspricht im ersten Schema für BA aus $BD+DI+IF+FC+CA=70.1$; aus $BI+IA=45.1$, aus $BC+CA=55.0$, etc.

In gleicher Weise könnte man natürlich auch ein double crossover Experiment berechnen und erhielte z. B. für den Versuch, BDC die Zahlen

67% non-crossover
 10% crossover DC
 20% crossover BD
 3% double crossover BDC

Es sei dies aber nicht weiter ausgeführt, einmal, weil wir glauben, dass die STURTEVANT'schen Vergleichszahlen auf Grund einer falschen Formel berechnet sind, und sodann weil es, wie so oft schon hervorgehoben, gar nicht unsere Absicht ist, das hier benutzte Schema an Stelle des MORGANSchen setzen zu wollen.

MORGAN weist nun noch als besonders beweiskräftig auf die Tatsache hin—inzwischen von MULLER im einzelnen ausgearbeitet,—dass bei der Spaltung von Bastarden von der Zusammensetzung $ABCDEFGGabcdeffg$ immer ganze Faktorengruppen beisammen bleiben, also meist single Crossing over, nur selten double und triple Crossing over eintritt. Eine Berechnung nach unserer Formel zeigt, dass auch dies als eine mathematische Konsequenz daraus abgeleitet werden kann, wie ja schon die Berechnung für das double Crossover zeigt. In MULLERS—zweifelloso—höchst schwierigen—Experimenten findet sich bereits für triple Crossing

over nur 1 Individuum. Nur bei viel grösseren Zahlen könnte man also die höheren crossover Klassen erwarten. Es braucht schliesslich wohl kaum hervorgehoben zu werden, dass der Erklärungswert von MORGANS Hypothese in Bezug auf multiplen Allelomorphismus und ähnliche Erscheinungen nicht dadurch berührt wird, wenn statt "Locus" Kräfte-relation steht.

Zum Schluss dieses Abschnitts noch eine Bemerkung. Es könnte jemand auf den Gedanken kommen, nach meinen Auseinandersetzungen die Auflösungsformel zu berechnen und danach die Werte p der obigen Formel für die von MORGAN gelieferten Zahlen zu berechnen, und dann vielleicht Inkongruenzen im Resultat als Widerlegung der hier vorgebrachten Anschauungen aufzuzeigen. Das wäre aber ein grobes Missverständnis. Ich habe, um meine These durchzuführen, möglichst einfache mathematische Voraussetzungen angenommen. Es liegt mir aber durchaus fern zu behaupten, dass gerade diese der Wirklichkeit entsprechen. Im Gegenteil ist es ja meine Hoffnung, dass die Betrachtung der empirischen Zahlen umgekehrt einmal die richtige Formel für die zu Grunde liegenden Kräfte und damit ihre physikalisch-chemische Zuweisung ermöglichen werde. Das, um was es sich mir handelt, ist vielmehr, wie schon oben gesagt, zu zeigen, dass es besser ist, sich nicht auf die grobsinnlichen Anschauungen über die Lage der Faktoren im Chromosom festzulegen, sondern MORGANS diagrammatische Darstellung nur als eine geometrische Ausdrucksform für Kräfte-relationen zu nehmen, deren Wesen zukünftiger Erkenntnis vorbehalten bleibt.

IV

Ist die Möglichkeit einer Erkenntnis dieser unbekannten Kräfte nun etwas in unendlicher Ferne liegendes? Ich glaube nicht. Und damit begeben wir uns nun auch auf den Weg der Hypothese. Wenn wir auch noch keine definitive Kenntnis darüber besitzen, was die Erbfaktoren darstellen, so machen eine Reihe neuer Arbeiten (z.B. LOEB u. CHAMBERLIN 1915, ONSLOW 1915, GOLDSCHMIDT 1916) es wahrscheinlich, dass sie etwas mit der Gruppe der Enzyme zu tun haben. Nun ist es ja eine unter Morphologen weitverbreitete Anschauung, dass Erbsubstanz chemisch mit Chromatin identisch sei. Ich habe dies, angesichts der cytologischen Tatsachen über die Umwandlungen des Chromatins in den Geschlechtszellen nie recht glauben können. Und auch die physiologischen Chemiker haben gewichtige Gründe dagegen. Nun findet man aber in der Fermentliteratur die Tatsache verzeichnet, dass einmal die

Enzyme besser Schädigungen widerstehen in Gegenwart von Nucleoproteiden, sodann, dass Oxydasen ebenso wie hydrolytische Fermente oft an Nukleoproteide gebunden sind. So liegt der Gedanke nahe, dass die Aufgabe des Chromatins es ist, die Vererbungsenzyme zu adsorbieren, als ihr Skelet zu dienen.¹ Sollten nicht vielleicht hinter den Variablen und Konstanten des Crossing over die Variablen und Konstanten der Adsorptionsgesetze stecken? Schon eine oberflächliche Orientierung in diesem so anziehenden Gebiet (s. etwa die Bücher von BAYLISS 1911, BECHHOLD 1912, MICHAELIS 1909, COHNHEIM 1912, EULER-POPE 1912) zeigt, wie aussichtsvoll eine eingehende Betrachtung dieser Beziehungen ist. Es sei nur erwähnt, welches Licht eine derartige Betrachtungsweise auf die typischen Oberflächenwandlungen des Chromatins während der Synapsis und Wachstumsperiode werfen könnte. Und der Weg hier weiterzukommen ist sicher ein sehr einfacher. Exakte Untersuchungen über den Einfluss verschiedener Temperaturen auf die Crossoverzahlen könnten vielleicht schon die entscheidenden Werte liefern.

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¹ Ich hatte vor mehr als einem Jahr das Vergnügen, diese hier in wenigen Worten angedeuteten Anschauungen über die chemische Basis der Vererbung A. P. MATHEWS auszuführen. Worauf er mich darauf hinwies, dass er genau die gleiche Anschauung in einem im Drucke befindlichen Werk ausgesprochen habe. Dies Buch (Physiological Chemistry, New York, 1915) ist inzwischen erschienen und enthält p. 175-182 die betreffenden sehr interessanten Ausführungen.

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THE NUMERICAL RESULTS OF DIVERSE SYSTEMS OF BREEDING, WITH RESPECT TO TWO PAIRS OF CHARACTERS, LINKED OR INDEPENDENT, WITH SPECIAL RELATION TO THE EFFECTS OF LINKAGE¹

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¹ From the Zoölogical Laboratory of the JOHNS HOPKINS UNIVERSITY.

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I. GENERAL, DEFINITIONS, METHODS

In an earlier paper (JENNINGS 1916) the present author has given formulae for the results of various systems of breeding, with respect to a single pair of characters.¹ When more than one pair are considered, the distribution of characters that Mendelism seemed to give has been greatly modified by the further discovery that characters may be linked. A first and perhaps practically most important step in determining the actual distribution is to deal numerically with two pairs of characters, linked or independent; this is what the present paper undertakes. The problem is to discover formulae which for a given system of breeding will give in later generations the proportions of the different classes of individuals (zygotes) with respect to two pairs of characters, when we know the constitution of the original progenitors. The present paper deals with: random mating; selection with respect to a single character (dominant or recessive); assortative mating with respect to a single character; and self-fertilization. Inbreeding is reserved for separate treatment. Only typical characters, not sex-linked, are dealt with.

(1) DESIGNATION OF FACTORS

The two members of a pair of alternative factors will be designated A and a ; of a second pair, B and b , the capital letter representing in

¹ Certain points in this earlier paper require mention or correction:

- (1) In section (8), page 65, the values given for AA , aa and Aa , hold for *any* later generation; the constitution of the population does not change with later matings, as stated in the text. This was pointed out to me independently by Dr. C. H. DANFORTH and by Dr. SEWELL WRIGHT. A slip with this correction was enclosed with the reprints distributed. [In the meantime the matter has been fully discussed by WENTWORTH and REMICK (1916).—*Note added in correcting the proof.*]
- (2) Essentially the formulae of sections (35) and (36), page 73, had been given by DETLEFSEN (1914, p. 95). DETLEFSEN includes in n the first cross, so that his formulae are stated in slightly different terms. I regret that I overlooked DETLEFSEN's work, which contains much of great interest on the theoretical results of continued inbreeding.
- (3) In the example under section (28), page 70, the value for aa should be $85/144$ in place of $91/144$.
- (4) In table 1, series L, under "How formed," read " $B_n F_{n-1} G_{n-1}$."

each case the dominant factor. *In giving the constitution of an individual the juxtaposition of the letters will indicate the constitution of the gametes from which the individual was formed, and consequently at the same time the linkage, if there is linkage.* Thus the individual $ABab$ is formed from the gametes AB and ab , and if there is linkage, this is between A and B on the one hand, between a and b on the other. The individual $AbaB$ was formed from the gametes Ab and aB , and the linkage, if any, is between A and b on the one hand, a and B on the other.

(2) LINKAGE; DESIGNATION OF THE LINKAGE RATIO r

When two pairs of factors are dealt with, these may be independent or linked. In the former case any possible combination of the two pairs occurs in the gametes as frequently as any other. But when two factors are linked, the combinations found in the gametes which produced the given parents occur in the gametes produced by those parents more frequently than do other combinations. Thus, if the individual $ABab$ was produced by union of the two gametes AB and ab , then when this individual forms gametes, there will be more gametes of the constitutions AB and ab than of the constitutions Ab and aB .

We shall designate the linkage ratio by the letter r . This number r indicates therefore the number of gametes showing the same combination of factors that occurred in the foregoing generation of gametes, in proportion to 1 showing other combinations. Thus, if in the case just cited, there are produced 3 gametes of the constitution AB (or ab) to 1 of Ab (or aB), the value of the linkage ratio r is 3. It is practically important to observe that for the working out of numerical proportions, "independence" of factors is merely a special case of linkage,—the particular case in which the value of the linkage ratio r is 1. Thus, if we derive general formulae for the results of linkage, these will include also the results when the factors are independent; in the latter case for numerical results it will merely be necessary to give to the letter r the value 1. As is well known, the value of r , the linkage ratio, may vary in different cases from 1 up to 80 or 100, or more.

In certain known cases, where linkage occurs, it is complete in one sex, the two factors involved acting in that sex like a single one. Thus, from the parent $ABab$ there are produced in one sex but two sorts of gametes, AB and ab , in equal proportions, while the other sex gives $r AB : 1 Ab : 1 aB : r ab$. It is not certain that this completeness of the linkage in one sex holds for all organisms, so that we shall deal both

with this case, and the case in which linkage is the same in both sexes.

The relative frequency with which the different gametes are formed of course affects the frequency with which individuals (zygotes) with particular combinations of factors appear in the next generation. Our task is to discover general formulae for the proportions of the different classes of zygotes with respect to two characters, whatever the degree of linkage; formulae from which numerical results are obtainable when the proper values are substituted for r . The solution of this problem is quite independent of the question of the cause of linkage. It merely requires that there shall be in each case some fairly constant average ratio between the number of gametes which show the original combinations and those which show the new combinations; the work of many investigators has shown that this is the case.

When two pairs of factors are dealt with, whether linked or independent, it is not possible from a knowledge of the constitution of the zygotes with respect to each pair taken separately, to tell how the two pairs will be combined; the rules of combination must be worked out for themselves. This principle will receive illustration in the present paper (see section (21)).

(3) METHOD

With respect to two pairs of factors there are 4 diverse sorts of gametes, AB , Ab , aB and ab . The combinations of these 4 kinds of gametes give 16 diverse kinds of zygotes; these and their origin from the gametes are illustrated in table 6. Owing to this considerable number of diverse kinds of zygotes, direct formulae for the zygotes of a later generation in terms of those of an earlier generation become complex, unless we begin with parents of a single simple type. On this account it is, wherever possible, simpler to break the computation into two steps: (1) to obtain the proportions of the four different kinds of gametes derivable from the given zygotes; (2) from the gametic proportions thus reached, the proportions of the different sorts of zygotes for the next generation are obtained. We shall therefore present formulae for each of these steps, and the computations for any particular case will usually require the use of both these formulae, save in special cases where it is possible to develop single, more comprehensive, formulae.

This method of proceeding by two steps (first finding the gametes, then from these the zygotes) depends upon the principle that *random mating of zygotes gives the same results as random mating of the*

gametes which they produce. The particular way in which the gametes have been united in the parental zygotes does not affect the results of random mating. This principle is easily demonstrated algebraically.

Where the mating is not at all at random, as in self-fertilization, the principle cannot be employed; we must devise formulae for the direct transformation of one generation of zygotes into a later one.

(4) TWO CLASSES OF FORMULAE; GENERAL AND SPECIAL

Two classes of formulae are obtainable:

General formulae for transforming generation n into generation $n + 1$. One class is of *general* application, so that whatever the constitution of the parental population, by means of the formulae the constitution of the population in later generations is obtainable. For example, the original population may be composed of diverse individuals in the proportions $3 ABAB + 1 abab + 1 AbaB + 4 ABaB$, and we may desire to know the constitution of the population in some later generation after breeding by random mating or assortative mating, or the like. Such general formulae can as a rule be given only for determining the constitution of the next following generation; the formulae can then be reapplied for determining the constitution of the next generation, and so on indefinitely. Thus such general formulae may be characterized as formulae for transforming generation n into generation $n + 1$.

Special formulae for parents $ABab$, etc. The second class consists of special formulae, for important particular cases, the main such case being that in which the original parents are all alike and are of the type $ABab$ or $AbaB$. For such parents, which represent the case to which the formulae will most commonly be applied, it is possible, for some systems of breeding, to obtain formulae that will give directly the constitution of the population in any later generation, without working out the constitution in the intervening generations. For example, if the original progenitors are $ABab$, we may by a proper formula determine at once what will be the constitution of the population after seven successive random matings, or ten successive self-fertilizations, or the like.

(5) ORDER OF TREATMENT

We shall first set forth the different classes of zygotes and gametes with respect to two pairs of factors, and propose algebraic designations for the proportional numbers in which each occurs in any case.

We shall then take up the derivation of the general and special formulae for each system of breeding, dealing separately with the cases

in which linkage is the same in the formation of both sorts of gametes, and that in which linkage is complete in forming one of the sets of gametes. The formulae derived will be grouped in a series of numbered tables, which for convenience of reference will be placed all together at the end of the paper.

(6) CLASSES OF ZYGOTES WITH RESPECT TO TWO PAIRS OF FACTORS, AND THEIR DESIGNATIONS

With respect to two pairs of factors, and having regard to linkage, there are ten diverse types of zygotes, the origin of which is illustrated in table 6. Any or all of these ten types may be included, in various proportions, in any population. The proportional numbers of these various classes of zygotes in any generation will be designated by the letters *c* to *l*, with the significations shown in table 1 (page 141). In table 1 we classify as homozygotes those that are homozygotic with respect to both pairs of factors; as heterozygotes those heterozygotic with respect to both pairs of factors; as mixed those homozygotic with respect to one pair, heterozygotic with respect to the other. Any population may be represented by table 1, when proper values are given to the letters *c* to *l*.

In the later treatment the letters *c* to *l* will be used to designate in brief the proportions of the various types of zygotes to which the given letter is assigned in this table 1; thus, *g* will be understood to signify always the number of zygotes having the constitution *ABab*; *j* the number of *ABaB*, etc. In specific cases the values of *c* to *l* will be diverse. Thus in the population composed of 3 *ABAB* + 1 *abab* + 1 *AbaB* + 4 *ABaB*, the value of *c* is 3, *f* = 1, *h* = 1, *j* = 4, while the value of the other letters is 0.

(7) CLASSES OF GAMETES WITH RESPECT TO TWO PAIRS OF FACTORS, AND THEIR DESIGNATIONS

There are four classes of gametes with respect to two pairs of factors. We shall designate their (relative) numbers in any given case by the letters *p*, *q*, *s* and *t*, with the significations shown in table 2 (page 141).

As in the case of the zygotes, so here, the letter *p* will at times be used by itself to designate the number of gametes of the type *AB*, *q* the number of *Ab*, etc.

II. RANDOM MATING

We shall first obtain formulae for the proportional numbers of the different sorts of gametes produced by any population of zygotes (of

generation n) ; these will be the gametes for producing generation $n + 1$.

Next we shall get formulae for the zygotes (of generation $n + 1$) resulting from the random mating of this (or of any) set of gametes.

Third, we shall develop formulae by which the proportions of the gametes for the next following generation may be obtained when we know the proportions of the gametes for the foregoing generation,—so that the proportions of the zygotes may be omitted from consideration until the generation is reached for which the zygotic proportions are desired.

Finally we shall take up special formulae for particularly important cases, such as that in which the original parents are all $ABab$ or $AbaB$.

DERIVATION OF THE PROPORTIONS OF THE DIFFERENT KINDS OF GAMETES PRODUCED BY ANY KNOWN SET OF ZYGOTES

Any population of zygotes may be represented in the way shown in table 1, by giving proper values to $c \dots l$. Our present question is: What will be the relative numbers of the four different sorts of gametes produced by such a population? Or since the relative proportions of the four sorts of gametes are designated by the letters p, q, s and t (table 2), what we require is to derive the values of p, q, s and t in terms of c to l (of table 1).

In deriving the gametes from the zygotes, it is to be remembered that the original gametic union that produced the zygotes of table 1 (and hence the linkage), is indicated by the juxtaposition of the letters, and that the linkage ratio is r .

$$(8) \text{ LINKAGE RATIO} = r$$

Taking first one of the heterozygotes, as $ABab$, the gametes are $r AB : 1 Ab : 1 aB : r ab$. In order to realize these proportions it is evidently necessary that each such zygote should produce $2r + 2$ gametes. To keep the proportions correct throughout, each gamete of table 1, whatever its constitution, must be considered to produce $2r + 2$ gametes, although from a homozygote these will all be alike, and from a mixed zygote there will be but two sorts, in equal numbers. We shall therefore find that the zygotes of table 1 give the gametes shown in the first column of table 3.

Having obtained table 3, we collect from the column "linkage = r " the various values for each of the four kinds of gametes AB, Ab, aB and ab . As in table 2, the total values for the different kinds are to be designated p, q, s and t , respectively. By collecting we obtain table 4.

(9) LINKAGE COMPLETE

In the case that the linkage is complete in forming one of the sets of gametes, the proportions of the gametes of that set will not be those in table 4. Where linkage is complete, each parent zygote produces but two kinds of gametes in equal number,—these being the same two kinds by which this parent was formed. Thus the individual *ABab* produces gametes *AB* and *ab* in equal numbers; the individual *AbaB* produces *Ab* and *aB*, etc. To get the correct proportions throughout we require to assume only that each zygote produces two gametes. The results are given in the second column of table 3. Collecting the values for the four sorts of gametes, and calling their proportions, when linkage is complete, by the capital letters *P*, *Q*, *S* and *T*, in place of the corresponding small letters, we obtain table 5.

(10) DETERMINATION OF THE PROPORTIONS OF THE DIFFERENT CLASSES
OF ZYGOTES PRODUCED BY THE RANDOM MATING OF
ANY SET OF GAMETES

The population at the beginning is that shown in table 1 (which of course represents any population whatever, if the correct values are given to the letters *c* to *l*). The proportions of the gametes (that is, the values of *p*, *q*, *s* and *t*) are determined by table 4.

Having thus obtained the values of *p*, *q*, *s* and *t*, we must next observe the zygotes produced by the random mating of the four sets of gametes, *p* . *AB*, *q* . *Ab*, *s* . *aB* and *t* . *ab*. The mating and results are represented in table 6.

It will be observed that of the resulting zygotes (table 6), the four forming the diagonal from the left upper corner to the right lower corner are homozygotes; the four forming the other diagonal are heterozygotes, and the other eight are mixed. The zygotes resulting from the first random mating ($n = 1$) are therefore those shown in table 7.

Table 7 is the fundamental general table for determining the zygotic proportions resulting from the random mating of any given set of gametes. It will be employed in working out the results of selection and of assortative mating, as well as of random mating.

Example. Tables 4 and 7 furnish the formulae for the two steps necessary to obtain the proportional numbers of the different classes of individuals (zygotes) in the generation $n + 1$, when we know those in generation n ,—the mating being at random, and the linkage being the same for both sets of gametes.

For example, suppose that the original population consists of 3 *ABAB* + 1 *abab* + 1 *AbaB* + 4 *ABaB*; that the linkage ratio r is 2, and that breeding is by random mating. What various types of individuals will be present in the next generation, and in what proportions?

Here evidently (referring to table 1),—

$$c = 3, \quad f = 1, \quad h = 1, \quad j = 4$$

while d, g, i, k and l are 0. Therefore the gametes produced will be, by table 4 (since $r + 1 = 3$):

$$\begin{array}{rcl} p & = & 3 \cdot (6 + 4) + 1 = 31 \\ q & = & 2 \cdot 1 = 2 \\ s & = & 3 \cdot 4 + 2 \cdot 1 = 14 \\ t & = & 3 \cdot 2 + 1 = 7 \\ \hline p + q + s + t & = & 54 \end{array}$$

The gametes will therefore be in the proportions 31 *AB* : 2 *Ab* : 14 *aB* : 7 *ab*.

Then the zygotes of the next generation ($n + 1$) will be, by table 7, the following:

<i>ABAB</i> = 31^2 = 961	<i>AbaB</i> = $2 \cdot 2 \cdot 14$ = 56
<i>AbAb</i> = 2^2 = 4	<i>ABAb</i> = $2 \cdot 31 \cdot 2$ = 124
<i>ABaB</i> = 14^2 = 196	<i>ABaB</i> = $2 \cdot 31 \cdot 14$ = 868
<i>abab</i> = 7^2 = 49	<i>abAb</i> = $2 \cdot 2 \cdot 7$ = 28
<i>ABab</i> = $2 \cdot 31 \cdot 7$ = 434	<i>abaB</i> = $2 \cdot 14 \cdot 7$ = 196

By now substituting these values for c to l in table 1, and using anew tables 4 and 7, we may find the zygotic proportions for the third generation, and so on indefinitely. If desired the values for c to l may be reduced to decimal fractions in each case, giving all later proportions in decimals.

(11) DETERMINATION OF THE PROPORTIONS OF THE DIFFERENT CLASSES OF ZYGOTES PRODUCED WHERE ONE SET OF GAMETES FORMED WITH LINKAGE (r) (TABLE 4) MATES WITH ANOTHER SET WITH COMPLETE LINKAGE (TABLE 5)

This represents what appears to be the usual condition, where the gametes from one sex (eggs or sperm) are produced with linkage r , the other set with complete linkage.

In this case, as usual, the population at the beginning is that in table 1.

We determine by table 4 the values for p , q , s and t , and by table 5 the values for P , Q , S and T .

Now to obtain the zygotic proportions in the next generation, in table 6 we substitute in one of the columns of gametes the values P , Q , S and T for p , q , s and t ; then we multiply as before to obtain the 16 lots of zygotes. Having performed this operation and classified the results in the same way as was done for table 7, we obtain for the zygotic proportions the table 8.

Example. To transform the zygotes of generation n into those of generation $n + 1$, when linkage is complete in one set of the gametes, we therefore use successively the formulae of tables 4, 5 and 8. Suppose that we take the same example given in section (10), page 106, but assume that linkage is complete in one set of gametes.

Then by tables 4 and 5 the two sets of gametes are:

$$\begin{array}{ll} p = 31 & P = 10 \\ q = 2 & Q = 1 \\ s = 14 & S = 5 \\ t = 7 & T = 2 \end{array}$$

And by table 8 the individuals (zygotes) of the next generation ($n + 1$) are:

$$\begin{array}{ll} ABAB = 310 & AbaB = 24 \\ AbAb = 2 & ABAb = 51 \\ aBaB = 70 & ABaB = 295 \\ abab = 14 & abAb = 11 \\ ABab = 132 & abaB = 63 \end{array}$$

By substituting these values for c to l in table 1, we may determine the proportions of the different types of individuals in the next later generation, and so on. We may of course, if we prefer, reduce all the proportions to decimal fractions, and employ these decimals in working out results for later generations.

DERIVATION OF THE GAMETES PRODUCED BY THE NEXT GENERATION OF ZYGOTES (GENERATION $n + 1$), WHEN THE GAMETES PRODUCED BY THE FOREGOING GENERATION (GENERATION n) ARE KNOWN

If it be desired to determine the zygotic constitution of the population in some later generation (as for example the fifth), it saves much labor to deal for the intervening generations with the gametes alone. That is, by formulae to be set forth, we determine directly from the proportions of the gametes produced by generation 1 the proportions

of the gametes produced by generation 2; thence the gametic proportions from generation 3; thence those from generation 4, thence from 5. Only for this final generation do we determine the zygotic proportions.

Our problem is therefore to obtain p_{n+1} , q_{n+1} , s_{n+1} and t_{n+1} from p_n , q_n , s_n and t_n .

(12) *Linkage the same in both sets of gametes*

To derive our formulae, we first obtain the gametes from the original parents (generation n) by table 4; then from these gametes we derive the zygotes (generation $n + 1$) by table 7. From these zygotes, by the method of section (8) and table 3, we find that the gametes produced are the following:

<i>Zygotes of $n + 1$</i>	=	<i>Gametes from $n + 1$</i>
$p^2.ABAB$	=	$p^2.(2r + 2) AB$
$q^2.AbAb$	=	$q^2.(2r + 2) Ab$
$s^2.aBaB$	=	$s^2.(2r + 2) aB$
$t^2.abab$	=	$t^2.(2r + 2) ab$
$2pt.ABab$	=	$2pt.r.AB + 2pt.Ab + 2pt.aB + 2pt.r.ab$
$2qs.AbaB$	=	$2qs.r.Ab + 2qs.AB + 2qs.ab + 2ps.r.aB$
$2pq.ABAb$	=	$2pq.(r+1) AB + 2pq.(r+1) Ab$
$2ps.ABaB$	=	$2ps.(r+1) AB + 2ps.(r+1) aB$
$2qt.abAb$	=	$2qt.(r+1) ab + 2qt.(r+1) Ab$
$2st.abab$	=	$2st.(r+1) ab + 2st.(r+1) aB$

Collecting the values for the gametes AB , Ab , aB , and ab , (from $n + 1$), and removing from each the factor 2, we obtain the formulae given in table 9.

By the continued use of these formulae we may find the proportions of the different gametes produced by any later generation of random mating, without troubling to find the zygotic constitution in any generation save the final one in which we are primarily interested. At any time the zygotic constitution is found by the formulae of table 7.

(13) *Independent factors*

If the factors are independent ($r = 1$), the gametic formulae of table 9 may be simplified through the substitution of 1 for r , giving table 10.

Example. In the example given in section (10), the following values were found for p , q , s and t for the first random mating:

$$p = 31 \quad q = 2 \quad s = 14 \quad t = 7$$

Then by the formulae of the table 9 the values of p , q , s and t for the second random mating will be (when $r = 2$):

$$p = 3.31.47 + 2.31.7 + 2.14 = 4833$$

$$q = 3.2.40 + 2.2.14 + 31.7 = 513$$

$$s = 3.14.52 + 2.2.14 + 31.7 = 2457$$

$$t = 3.7.23 + 2.31.7 + 2.14 = 945$$

$$p + q + s + t = 3.54^2 = 8748$$

Now by the formulae of table 7, we may if we desire, obtain from these results the relative numbers of the different kinds of zygotes resulting from the second random mating.

Or we can by a repeated use of the formulae of the present section obtain the gametic constitution for the third, fourth and later generations; finding in addition the zygotic constitution for any desired generation.

(14) *Linkage complete in one sex, r in the other*

In this case we derive two sets of gametes from the original parents, by means of tables 4 and 5, and these give for generation $n + 1$, the zygotes of table 8. From these zygotes of table 8, we must find two sets of gametes, one with linkage r (by the method illustrated in section (8)), the other with complete linkage (by the method illustrated in section (9)). We must assume that both sexes are represented in each kind of zygote of table 8, so that we must form a first set of gametes from all the kinds of zygotes of table 8 by the method of section (8), then a second set from all by the method of section (9). Performing these operations and collecting the results, we obtain table 11.

In comparing the gametes of set 1 with those of set 2 (in table 11) certain constant relations between the two sets become evident. These are shown in table 12. These relations are of consequence for certain problems, particularly in selection and assortative mating; they are also useful in checking up the correctness of computations.

Example. We will take the example employed in section (10), but now assuming that linkage is complete in one sex. The parent zygotes were 3 $ABAB$ + 1 $abab$ + 1 $AbaB$ + 4 $ABaB$; and $r = 2$.

As shown in section (10), before the first random mating the gametes of the first set, with linkage r , are:

$$p = 31 \quad q = 2 \quad s = 14 \quad t = 7$$

According to section (11), further, the gametes of the second set, with complete linkage, are:

$$P = 10 \quad Q = 1 \quad S = 5 \quad T = 2$$

The zygotes resulting from the first random mating are therefore, by table 8:

$$\begin{array}{ll} ABAB = 31.10 = 310 & AbaB = 1.14 + 2.5 = 24 \\ AbAb = 2.1 = 2 & ABAb = 10.2 + 31.1 = 51 \\ aBaB = 14.5 = 70 & ABaB = 10.14 + 31.5 = 295 \\ abab = 7.2 = 14 & abAb = 1.7 + 2.2 = 11 \\ ABab = 10.7 + 31.2 = 132 & abaB = 5.7 + 14.2 = 63 \end{array}$$

The gametes for the second random mating ($n = 2$) are obtained from the values of p_1, q_1 , etc., given above, by the formulae of table 11, giving the following:

Set 1: Linkage $r = 2$, in both sexes:

$$\begin{array}{l} p_2 = 3.31.16 + 3.10.47 + 2.(70 + 62) + 14 + 10 = 3186 \\ q_2 = 3.2.13 + 3.1.40 + 2.(14 + 10) + 70 + 62 = 378 \\ s_2 = 3.14.17 + 3.5.52 + 2.(14 + 10) + 70 + 62 = 1674 \\ t_2 = 3.7.8 + 3.2.23 + 2.(70 + 62) + 14 + 10 = 594 \\ \hline p + q + s + t = 5832 \end{array}$$

Set 2: Linkage complete in one sex:

$$\begin{array}{l} P_2 = 10.54 + 31.18 = 1098 \\ Q_2 = 1.54 + 2.18 = 90 \\ S_2 = 5.54 + 14.18 = 522 \\ T_2 = 2.54 + 7.18 = 234 \\ \hline P + Q + S + T = 1944 \end{array}$$

It will be observed that the sum ($p + q + s + t$) is just 3 times the sum of ($P + Q + S + T$), 3 being the value of ($r + 1$).

Now by table 8 we may if we desire find the proportions of the different zygotes resulting from the second random mating; or we may omit this, and find directly the two sets of gametes for the third random mating; and so on.

RANDOM MATING: SPECIAL FORMULAE

(15) *Parents all ABab*

For the specially important case in which the parents are a first cross between *ABAB* and *abab*, (so that they are themselves *ABab*), we may obtain a general formula which shall give us directly the proportions of gametes (and indirectly of zygotes) for producing any generation *n*, without working out the proportions for intervening generations. For this the following points must be noticed:

Evidently the number of gametes *AB* is the same as the number of *ab*; while the number of *Ab* is the same as of *aB*, and this equivalence will be found to hold throughout random mating. We have therefore, so far as the gametes go, but two unknown quantities to deal with in place of four. In tables 2 and 5, therefore, we can put:

$$p = t \quad P = T \quad q = s \quad Q = S$$

We require therefore but to find *p*, *P*, *q* and *Q*; these will give us the others.

Now, if at the beginning the parents are all *ABab*, and the linkage ratio is *r*, then evidently the gametes from these parents are *r AB* : 1 *Ab* : 1 *aB* : *r ab*, so that for producing generation 1 the gametes are:

$$p = r \quad q = 1 \quad p + q = r + 1 \quad p - q = r - 1$$

In the sex (if there is such) in which the linkage is complete, the gametes formed by *ABab* are evidently simply *AB* and *ab* in equal numbers, so that (for producing generation 1):

$$P = 1 \quad Q = 0 \quad P + Q = 1 \quad P - Q = 1$$

(16) Linkage *r* in both sets of gametes, parents all *ABab*

Now, if we take first the case in which linkage is *r* in both sexes, we may by table 9 from the above gametic proportions for producing generation 1 determine the gametic proportions for producing generation 2. We shall find these to be as follows:

$$\begin{aligned} p_2 &= 2r^3 + 3r^2 + 2r + 1 = (r + 1)(2r^2 + r + 1) \\ q_2 &= 3r^2 + 4r + 1 = (r + 1)(3r + 1) \end{aligned}$$

Since it is the relative proportions that we desire, we can take out the common factor $(r + 1)$, and we have:

$$\begin{aligned} p_2 &= 2r^2 + r + 1 \\ q_2 &= 3r + 1 \\ p_2 + q_2 &= 2r^2 + 4r + 2 = 2(r + 1)^2 \\ p_2 - q_2 &= 2r^2 - 2r = 2(r^2 - r) \end{aligned}$$

If we continue in this way, finding successively the values of $p_3, p_4, p_5, q_3, q_4, q_5$, etc., certain general relations manifest themselves, particularly with regard to the sums of p and q , and their differences. It turns out that for producing any generation n

$$\begin{aligned} p_n + q_n &= 2(r + 1)^n \\ p_n - q_n &= 2(r^n - r^{n-1}) \end{aligned}$$

Solving these two equations for the values of p_n and q_n (and omitting from the result the common factor, 2), we obtain the formulae of table 13.

Having determined the values of p_n, q_n, s_n and t_n by table 13, the proportions of the different classes of individuals (zygotes) in generation n is obtained from table 7.

(17) If there is no linkage ($r = 1$) and the parents are all $ABab$ the population will be found to remain constant, in the following proportions:

The four sorts of homozygotes, each = 1

The two sorts of heterozygotes, each = 2

The four sorts of mixed, each = 2

Example. Parents all $ABab$, linkage ratio $r = 3$. What will be the constitution of the population (zygotes) after 4 random matings? By table 13:

$$p_4 (= t_4) = 4^4 + 3^4 - 3^3 = 310$$

$$q_4 (= s_4) = 4^4 - 3^4 + 3^3 = 202$$

$$p^2 (= t^2) = 96,100$$

$$q^2 (= s^2) = 40,804$$

$$2pq (= 2st) = 125,240$$

$$\text{Total zygotes} = (620 + 404)^2 = 1024^2 = 1,048,576.$$

From which it is evident that by the zygotic formulae of table 7 the proportions of the different sorts of zygotes are:

$$ABAB = \frac{96,100}{1,048,576} = .0916$$

$$abab = .0916$$

$$AbAb = .0389$$

$$aBaB = .0389$$

$$\text{Total homozygotes} = .2611$$

$$ABab = .1833$$

$$AbaB = .0778$$

$$\text{Total heterozygotes} = .2611$$

$$\text{Each of 4 sorts of mixed} = .1194.$$

$$\text{Total mixed} = .4778$$

(18) Parents all $ABab$; linkage r in one set of gametes, complete in the other

Here, as in section (15), the number of gametes AB is equal to that of ab , while the number of Ab is equal to that of aB , so that:

$$p = t \quad q = s \quad P = T \quad Q = S$$

Also, as we saw in (15), for the first mating ($n = 1$):

$$p = r \quad q = 1 \quad P = 1 \quad Q = 0 \\ p + q = r + 1; \quad p - q = r - 1; \quad P + Q = 1; \quad P - Q = 1.$$

Now by the use of table 11, we obtain the corresponding values of p , q , P and Q for producing generation 2. We find thus that:

$$\begin{array}{ll} p_2 = 2r^2 + 2r + 1 & P_2 = 2r + 1 \\ q_2 = 2r + 1 & Q_2 = 1 \\ p_2 + q_2 = 2(r + 1)^2 & P_2 + Q_2 = 2(r + 1) \\ p_2 - q_2 = 2r^2 & P_2 - Q_2 = 2r \end{array}$$

Now if by continued use of table 11, we find the corresponding values for successive generations, we discover that for any number n of generations the gametes which mate to form that generation show the following relations:

$$\begin{array}{l} p_n + q_n = 2^{n-1} (r + 1)^n \\ p_n - q_n = 2r^2 (2r + 1)^{n-2} \\ P_n + Q_n = 2^{n-1} (r + 1)^{n-1} \\ P_n - Q_n = 2r (2r + 1)^{n-2} \end{array}$$

Solving these equations for the values of p , q , P and Q , we obtain the formulae of table 14.

Having determined thus the proportions of the gametes, the constitution of generation n in zygotes is obtained by the use of table 8.

Example.—Parents $ABab$; linkage ratio $r = 3$; four generations of random mating ($n = 4$). What is the constitution of the population? By table 14, the gametic proportions preliminary to generation 4 will be:

$$\begin{array}{ll} p_4 = 2^2 \cdot 4^4 + 9 \cdot 7^2 = 1465 \\ q_4 = 2^2 \cdot 4^4 - 9 \cdot 7^2 = 583 \\ p_4 + q_4 = 2048 \\ P_4 = 2^2 \cdot 4^3 + 3 \cdot 7^2 = 403 \\ Q_4 = 2^2 \cdot 4^3 - 3 \cdot 7^2 = 109 \\ P_4 + Q_4 = 512 \end{array}$$

To obtain the zygotes resulting from the mating of these gametes it is well to note the following:

$$\begin{aligned}
 Pp &= 590,395 \\
 Qq &= 63,547 \\
 Pq &= 234,949 \\
 pQ &= 159,685 \\
 Pp + Qq + Pq + pQ &= 1,048,304
 \end{aligned}$$

Then by table 8 (remembering that $p = t$, $q = s$, $P = T$ and $Q = S$), we find that the total number of zygotes ($P + Q + S + T$) ($p + q + s + t$) is 4,194,304. Working out, by table 8, the proportions for each of the classes of zygotes, and dividing each by 4,194,304 in order to reduce them to decimals, we find that the population in the fourth generation is:

Homozygotes, <i>ABAB</i> and <i>abab</i> , each	.141
<i>AbAb</i> and <i>aBaB</i> , each	.015
Total	.312
Heterozygotes, <i>ABab</i>	.282
<i>AbaB</i>	.030
Total	.312
Mixed, four sorts, each	.094
Total mixed	.376

(19) *Parents AbaB; linkage r in both sets of gametes*

In this case simply interchange the values of p and q in table 13 (of course therefore also the values of t and s), then obtain the zygotic proportions by table 7.

(20) *Parents AbaB; linkage r in one set of gametes, complete in the other*

In this case simply interchange the values of p and q ; also of P and Q , in table 14 (of course therefore also the values of t and s , as well as of T and S); then obtain the zygotic constitution by table 8.

(21) *Original parents ABAB and abab in equal numbers, random mating*

In this case if there is linkage the proportions of gametes and zygotes for any generation must be worked out by the general formulae for random mating, given in sections (8) to (14).

When there is no linkage ($r = 1$) it is instructive to compare this

case with that in which the parents are all *ABab* (and there is no linkage). If we examine the results with respect to single pairs of characters taken separately, we find them to be identical for the two cases. That is, when the parent population is either *ABab*, or is *ABAB + abab*, random mating gives for all later generations with respect to one pair of characters the uniform constitution $\frac{1}{4} AA + \frac{1}{2} Aa + \frac{1}{4} aa$; with respect to the other the constitution $\frac{1}{4} BB + \frac{1}{2} Bb + \frac{1}{4} bb$. But when we consider the two pairs together, we find that the two cases give diverse results; the two pairs of characters are combined diversely in the two cases. This is therefore an example of the fact, mentioned in section (2), that we cannot from a knowledge of the constitution with respect to two pairs of characters taken separately determine what will be the constitution with respect to combinations of the two pairs. In the case of the population derived from the random mating of *ABab*, the proportion of any combination of the two pairs is merely the product of the proportions for the two component pairs taken separately, thus the proportion that are *AABb* is $\frac{1}{4} \times \frac{1}{2} = \frac{1}{8}$, etc. But when the original parents are *ABAB + abab*, this rule does not hold. The gametes from such parents are in any generation n the following:

$$p_n = t_n = 2^{n-1} + 1$$

$$q_n = s_n = 2^{n-1} - 1$$

The zygotic proportions are then obtainable by table 7. It will be found that these zygotic proportions change from generation to generation, although for each pair of characters taken by itself the proportions are constant. The zygotic proportions in successive generations are:

Random matings	1	2	3	n
<i>ABAB</i> and <i>abab</i> , each	4	9	25	D_n^2
<i>AbAb</i> and <i>aBaB</i> , each	0	1	9	C_{n-1}^2
<i>ABab</i>	8	18	50	$2D_n^2$
<i>AbaB</i>	0	2	18	$2C_{n-1}^2$
Mixed, 4 sorts, each	0	6	30	$2D_n C_{n-1}$

For the n 'th generation the proportions are above given in terms of the series of table 1 in my earlier paper (JENNINGS 1916); thus the value for *ABAB* and *abab* is the square of the n 'th term of series D of that paper; the value for *AbaB* is twice the square of the $(n - 1)$ th term of series C of that paper, etc.

III. SELECTION WITH RELATION TO A SINGLE CHARACTER

Suppose that in breeding, selection is exercised with respect to a single character forming one of a pair; for example suppose that of the pair A and a , individuals showing the character A are always selected for further propagation. In our previous contribution (JENNINGS 1916) we have dealt with the results on the constitution of the population with respect to this pair on which selection is based. But what will be the effect on the constitution with respect to another pair of factors, B and b , which is linked with the pair on which selection is based? That is, in a population composed of individuals having A , a , B and b in the various possible combinations, what will be the resulting constitution due to selecting for the character A for a given number n of generations?

We shall take up first the case in which the selected character is dominant, next that in which it is recessive. We may proceed upon the same general plan employed for random mating, employing primarily the proportions of gametes in the successive generations as the bases for our work, and deriving the proportions of zygotes secondarily from those for the gametes that produce them.

SELECTION OF DOMINANTS WITH RESPECT TO ONE OF THE PAIRS OF CHARACTERS; GENERAL FORMULAE

(22) *Gametes produced when there is selection of dominants with respect to one pair*

If we have such a population as is shown in table 1, and breed only from those that are dominants with respect to the pair A and a , this is equivalent to omitting all the zygotes that do not contain A ; that is, it omits c , f and l of table 1. The gametes produced when there is such selection of dominants are therefore in the proportions shown in table 15 (compare with tables 4 and 5).

(23) *Proportions of the different classes of zygotes produced in the next generation ($n + 1$), when the breeding is by selection for dominant A*

The selection has taken place in the production of the gametes (table 15). These gametes now simply mate at random, so that we can employ directly the tables 7 and 8, for random mating. Therefore when there is selection for dominant A , the procedure for finding the proportions of the population in the next generation is as follows:

First give the proper values to the letters c to l , in table 1, and to r .

If linkage is the same ($=r$) in both sets of gametes, employ first the formulae of table 15, (set 1); then those of table 7; this gives the different classes of individuals in the next generation $n + 1$.

If linkage is complete in one set of gametes, employ first table 15 (both sets), then table 8; thus obtaining the proportions of the different classes of individuals in the next generation ($n + 1$).

If it be desired to find the zygotic proportions only for some later generation (as for example the seventh), it is not necessary to find the zygotic proportions for the intervening generations, but one works for these intervening generations with the gametes alone, according to the methods of the following sections (24) and (25).

(24) *Derivation of the gametes produced by the next generation ($n+1$) of zygotes, when the gametes produced by the preceding generation n are known, (breeding by selection of dominant A)*

If we desire to obtain the zygotic proportions only for some later generation, we may work for the intervening generations only with the gametes, by methods analogous to those set forth for random mating

Linkage the same ($=r$) in both sexes. We use the method set forth in sections (12), (13) and (14).

in section (12), but exclude from gamete formation the zygotes $aBaB$, $abab$, and $abaB$ (since these do not contain A). We thus obtain the formulae given in table 16.

Of course the zygotic proportions for generation $n + 1$ may now if desired be found from the zygotic formulae of table 7. Or by repeated use of these formulae of table 16 we may find the gametic proportions for any later generation, then by table 7 find the zygotic proportions for that generation.

(25) *Linkage complete in one set, r in the other*

Derivation of the gametes that produce the succeeding generation ($n + 1$), from those that produce the preceding generation (n)

We use the methods set forth in (14), but exclude from gamete formation the zygotes $aBaB$, $abab$ and $abaB$ (since these do not contain A). The formulae we require are indeed obtained directly from those of table 11, by omitting in all cases the factors Ss , Tt , St and sT . The results are given in table 17.

By the repeated use of the formulae of this table 17, we may find the gametic proportions for any later generation; then by table 8 find

the zygotic proportions for that generation. See the example in section (27).

No formula has been found obtainable for determining the proportions in any given later generation n , without working out the values for the intervening generations. Even when the original parents are $ABab$ or $AbaB$, the general methods (22) to (25) must be employed. The most important case, in which the original parents are $ABab$, will be found worked out illustratively in section (27).

(26) SELECTION OF DOMINANTS WITH RESPECT TO ONE OF THE PAIRS OF
CHARACTERS; SPECIAL FORMULAE FOR THE EFFECT
ON THE OTHER PAIR

Possibly the most interesting question in selection with reference to one pair of characters is its effect on another pair of characters, linked with the first pair. We shall take this up here, giving formulae for both the single factor-pairs taken separately.

Proportions of the single factor-pairs taken separately, when there is selection of dominant A : From the formulae of table 15, or of tables 16 and 17, taken in connection with those of tables 7 and 8, as set forth in sections (22) to (25), we may readily obtain for the desired generation the proportions of the population with relation to the members of either pair of factors taken separately; that is, with relation to A and a ; or to B and b . After obtaining for the next generation the gametic proportions of table 16 (if linkage is the same in both sets); or those of table 17 (if linkage is complete in one of the sets of gametes), we observe that the gametic proportions for A and a , and for B and b , are those given in table 18.

The zygotic proportions in the next generation ($n + 1$) are then, with relation to the single factor-pairs taken separately, those given in table 19.

The same proportions for each pair separately would be obtained by deriving the zygotic proportions for the two pairs together according to (24) and (25), then tabulating the constitution with reference to the factors taken separately.

The formulae given in table 19 for AA , Aa and aa give the same results as are given in sections (19) to (24) of my earlier paper (JENNINGS 1916), in which a single pair of factors was considered by itself. The linkage of course has no effect on the proportions of the pair with reference to which selection is made.

With relation to BB , Bb and bb , the proportions depend on the amount of linkage; the formulae of the present section enable us to determine precisely how selection with reference to one character (A) affects the proportions with respect to another character linked with it (B and b). If there is no linkage ($r=1$), the formulae given in table 19 for BB , Bb and bb give the same results as for those of random mating (sections (1) to (12) in my earlier paper); that is, selection with reference to A and a is random mating with reference to B and b , if the two pairs are not linked.

All these matters are illustrated in the concrete example given in the following sections (27) and (28).

(27) Illustrative example of the results of selecting dominants;
parents all $ABab$

To illustrate the use of the formulae for selection of dominants, we will take the most important typical case, in which the parents at the beginning are the dihybrid $ABab$. We will determine the results for several generations of selecting for propagation only those having the dominant factor A . We shall compare the results when there is linkage and when there is none; also the results when linkage is alike in both sexes, and those when linkage is complete in one sex. To keep the numbers relatively small we shall assume the linkage to be 2.

As the original parents ($ABab$) all contain A , none are excluded in the first mating. When there is no linkage the gametes are evidently 1 AB : 1 Ab : 1 aB : 1 ab . When the linkage is 2, the gametes are 2 AB : 1 Ab : 1 aB : 2 ab .

No linkage ($r=1$). In this case for the first mating, as we have seen, $p_1=1$, $q_1=1$, $s_1=1$, $t_1=1$. We now find the proportions for the succeeding generations, by the formulae of table 16. For the next generation ($n=2$) they are evidently as follows (since $r+1=2$).

$$\begin{aligned} p_2 &= 2 \cdot 1 \cdot 3 + 1 \cdot 1 + 1 = 8 (=2) \\ q_2 &= 2 \cdot 1 \cdot 3 + 1 \cdot 1 + 1 = 8 (=2) \\ s_2 &= 2 \cdot 1 + 1 + 1 = 4 (=1) \\ t_2 &= 2 \cdot 1 + 1 + 1 = 4 (=1) \end{aligned}$$

As it is only the proportional numbers that we desire, we may divide through by 4, giving the numbers in the last column.

Repeating our use of the formulae of table 16, we find that when

there is no linkage the gametic proportions for the first four generations are:

n	=	1	2	3	4
p	=	1	2	3	4
q	=	1	2	3	4
s	=	1	1	1	1
t	=	1	1	1	1
		<hr/>	<hr/>	<hr/>	<hr/>
		4	6	8	10

In general, it appears that for any generation n , p and q are each equal to n , while s and t are each 1.

Linkage 2, alike in both sexes ($r=2$).

For generation 1, as we have seen, $p=2$; $q=1$; $s=1$; $t=2$. Applying now the formulae of table 16 and noting that $r+1=3$, the proportions for generation 2 are found to be the following:

$$\begin{aligned} p_2 &= 3 \cdot 2 \cdot 4 + 2 \cdot 4 + 1 = 33 = 11 \\ q_2 &= 3 \cdot 1 \cdot 5 + 2 \cdot 1 + 4 = 21 = 7 \\ s_2 &= 3 \cdot 2 + 2 \cdot 1 + 4 = 12 = 4 \\ t_2 &= 3 \cdot 2 + 2 \cdot 4 + 1 = 15 = 5 \end{aligned}$$

(We reduce to lowest integral terms by dividing all the proportions by 3.)

In the third generation, by renewed application of table 16, we find the proportions to be:

$$\begin{aligned} p_3 &= 3 \cdot 11 \cdot 22 + 2 \cdot 55 + 28 = 864 = 32 \\ q_3 &= 3 \cdot 7 \cdot 23 + 2 \cdot 28 + 55 = 594 = 22 \\ s_3 &= 3 \cdot 44 + 2 \cdot 28 + 55 = 243 = 9 \\ t_3 &= 3 \cdot 35 + 2 \cdot 55 + 28 = 243 = 9 \end{aligned}$$

(We divide through by 27 to reduce to lowest terms.)

Thus when r is 2 in both sexes, the gametic proportions for the first four generations are:

n	=	1	2	3	4
p	=	2	11	32	379
q	=	1	7	22	269
s	=	1	4	9	86
t	=	2	5	9	76
		<hr/>	<hr/>	<hr/>	<hr/>
		6	27	72	810

Linkage complete in one sex; $r = 2$. In the sex in which the linkage is r , the parents $ABab$ of course produce gametes in the proportions $2 AB : 1 Ab : 1 aB : 2 ab$; these form the gametes of set 1. In the sex in which linkage is complete, the gametes formed are evidently $1 AB : 0 Ab : 0 aB : 1 ab$ (set 2). Using the letters p, q, s and t for the set 1 and P, Q, S and T for set 2, the gametes for the first generation ($n = 1$) are therefore:

Set 1	Set 2
$p = 2$	$P = 1$
$q = 1$	$Q = 0$
$s = 1$	$S = 0$
$t = 2$	$T = 1$

To obtain the gametic proportions in preparation for the next generation, we begin with the values just given, and employ the formulae of table 17. We thus find that for $n = 2$:

Set 1	Set 2
$p_2 = 3 \cdot 2 \cdot 1 + 3 \cdot 1 \cdot 4 + 2 \cdot 4 + 0 + 0 = 26$	$P_2 = 1 \cdot 6 + 2 \cdot 2 = 10$
$q_2 = 3 \cdot 1 \cdot 2 + 3 \cdot 0 \cdot 5 + 2 \cdot 0 + 2 + 2 = 10$	$Q_2 = 1 \cdot 2 = 2$
$s_2 = 3 \cdot 1 + 2 \cdot 0 + 2 + 2 = 7$	$S_2 = 1 \cdot 1 = 1$
$t_2 = 3 \cdot 1 + 2 \cdot 4 + 0 + 0 = 11$	$T_2 = 1 \cdot 3 + 2 \cdot 1 = 5$
—	—
54	18

Repeating the use of the formulae of table 17, but now beginning with the values for $n = 2$, and so on, we find that for the first four generations the gametic proportions are as follows (under each value of n is given in the first set the value of p, q , etc., in the second the value of P, Q , etc.):

n	1		2		3		4	
	Set 1	Set 2	Set 1	Set 2	Set 1	Set 2	Set 1	Set 2
p and P ($= AB$) =	2	1	26	10	117	42	310	108
q and Q ($= Ab$) =	1	0	10	2	45	12	122	36
s and S ($= aB$) =	1	0	7	1	24	5	53	13
t and T ($= ab$) =	2	1	11	5	30	13	55	23
Totals	6	2	54	18	216	72	540	180

Having now obtained the gametic proportions for each of the three diverse cases, it is a simple matter to compute for any generation the

proportions of the ten different sorts of zygotes. For the cases where the linkage relations are the same in both sexes we use the formulae of table 7; for the case where linkage is complete in one sex we employ the formulae of table 8. The results for the four generations are given in table 20. In each generation the results are given for the three diverse linkage relations; where r is given as 1 there is of course no linkage; where $r=2$ the linkage ratio is 2 to 1 in both sexes; the third case, where the linkage is 2 to 1 in one sex and complete in the other, is indicated by putting $r=2+$.

The results for each case are given twice; first as whole numbers, as they will be obtained from the formulae; then as decimal fractions, for comparison with the other cases. For example, in the first place of the first column we find $1=.0625$. This means that out of the total 16 zygotes, one will be $ABAB$, and that this is equal to .0625 of the total.

(28) *The proportions for single factor-pairs taken separately; example:* In our example (27) we select entirely with reference to the pair A and a . The most interesting question doubtless is: What effect has this on the proportions of the various combinations of B and b , when the two pairs are linked?

This question may be answered from the formulae of table 19, employing the gametic proportions already given in table 20. We give the results for both the pairs, A and a , and B and b .

From table 19, the values are in the first generation:

When there is no linkage ($r=1$):

$$\begin{array}{lll} AA=4 & Aa=8 & aa=4 \\ BB=4 & Bb=8 & bb=4 \end{array}$$

When $r=2$:

$$\begin{array}{lll} AA=9 & Aa=18 & aa=9 \\ BB=9 & Bb=18 & bb=9 \end{array}$$

When $r=2+$ (linkage complete in one sex):

$$\begin{array}{lll} AA=1 & Aa=2 & aa=1 \\ BB=1 & Bb=2 & bb=1 \end{array}$$

Thus for this first generation all values of r give the same result for each of the combinations.

In later generations the results differ for the different values of r . Table 21 gives the proportions of the different combinations for the first four generations.

As table 21 shows, when there is linkage there is a steady increase in the proportion of BB over bb , as also of BB over Bb , as a result of selection for the character A .

SELECTION OF RECESSIVES

Only individuals *not* containing the factor A are selected for propagation. That is, selection is of individuals aa only.

We may deal at the same time with the two cases (1) where linkage is the same in both sexes, and (2) where linkage is complete in one sex, for the two give here the same results.

(29) *Gametes produced when there is selection of recessives with respect to one pair of factors*

Suppose that of the zygotes of table 1, only those that are recessive with respect to the pair A and a are bred, that is, only those that contain aa . In this case all zygotes are omitted except c , f and l . These give only gametes aB and ab , so that for the gametes we have only the proportions s and t to deal with. If we determine the gametic proportions in accordance with the principles in section (22), we find that

$$s = (r+1)(2c+1)$$

$$t = (r+1)(2f+1)$$

But as it is only the relative proportions that are important, we may divide both these by $(r+1)$, giving table 22.

Furthermore, if we determine the proportions for the two sorts of gametes when linkage is complete, we find them to be identical with those in table 22. This table therefore serves for the gametic proportions whether linkage is or is not complete.

(30) *Proportions of the different sorts of zygotes produced in the next generation ($n+1$), when the breeding is by selection of recessives aa*

Here, as in (23), the selection has occurred in the production of the gametes, and the gametes now mate at random. We can therefore employ directly the table for random mating. Since however in the case of selection of recessives the gametes are the same whether linkage is complete or not, we need to employ only table 7. But as only a few of the classes of zygotes of table 7 are formed, it will simplify matters to make a new table, including only those classes. This gives us table 23. Thus the total procedure in the case of selection of recessives aa is as follows:

Give the proper values to the letters c to l in table 1.

Employ first the formulae of table 22.

With the results from table 22 employ the formulae of table 23. These give the proportions of the different classes of individuals in the next generation $n + 1$.

(31) *Derivation of the gametes produced by the next generation $n + 1$ when the gametic proportions from generation n are known*

In the very first selection the factor A was entirely excluded and can never reappear, so that no farther selection occurs, and all future breeding is by random mating. The gametes p and q thus never appear. We may therefore apply directly the gametic formulae for random mating, as given in table 9, but including only those parts based on s and t alone. This gives us:

$$\begin{aligned}s_{n+1} &= (r+1)s(s+t) \\ t_{n+1} &= (r+1)t(s+t)\end{aligned}$$

But both the right hand members can be divided by $(r+1)(s+t)$, giving merely

$$\begin{aligned}s_{n+1} &= s_n \\ t_{n+1} &= t_n\end{aligned}$$

that is, the proportions of s and t are constant from generation to generation; it follows that the proportions of the three possible types of gametes given in table 23 are likewise constant from generation to generation.

Thus, in the case of selection of recessives with respect to the pair A and a , we require only to obtain for the first generation the values of s and t by the formulae of table 22; these values hold for all generations. We then obtain the proportions of the zygotes by the formulae of table 23, and these values likewise hold for all generations. If we carry through in detail an analysis in the case where linkage is complete in one sex, we come to the same result.

Put in another way, selection of recessives with respect to A and a gives random mating with respect to B and b , no matter what the linkage is, and no matter whether linkage is alike in both sexes, or is complete in one sex.

IV. ASSORTATIVE MATING WITH RESPECT TO ONE OF THE PAIRS OF CHARACTERS: DOMINANT WITH DOMINANT, RECESSIVE WITH RECESSIVE

(32) *General.* In assortative mating with respect to a single pair of characters (as A and a), all individuals containing A mate together at random; likewise all individuals not containing the factor A . The

most interesting question involved is: What is the effect of this on a second pair of factors (B and b), that are linked with the first pair? The proportions of all possible combinations of the two pairs must of course be determined.

Assortative mating is in some sense a combination of selection for dominants on the one hand, of recessives on the other, with of course continual subtraction of the recessive products from the dominant group, and their addition to the recessive group. The chief difficulty to be met is the necessity of keeping the proportions of the two groups correct with reference to each other; they cannot be dealt with separately. This adds some complications, and to meet the difficulty certain additional designations and classifications will be introduced.

The population at the beginning is that shown in table 1. We observe that in this population the classes c , d , g , h , i , j and k contain the dominant factor A ; it will be convenient to designate their sum by the letter D . The classes e , f , and l contain only the recessive factors aa ; the sum of these three classes will be called R . The sum of all ($D+R$) will be denominated N . For ease of reference we incorporate these in the numbered table 24.

PRODUCTION OF THE GAMETES IN ASSORTATIVE MATING

(33) For the production of gametes from the dominant zygotes (of table 1) we employ directly the formulae of table 15.

(34) For the production of gametes from the recessives we might use the formulae of table 22. It is needful, however, as will appear later, to use certain other designations for the gametic proportions in place of s and t (or S and T), in order to distinguish the gametes obtained from the recessives from those obtained from the dominants. We will therefore employ the Greek equivalents for those letters, using the lower case letters, as heretofore, for gametes formed with linkage r , the capital letters for those formed with complete linkage. This transforms table 22 into table 25. It will be observed that σ and Σ have the same values, as do also τ and T , but it is needful to distinguish them for the following reason. When we obtain the complete set of gametes from both dominants and recessives, one set formed with linkage r , the other set with complete linkage, either set may be reduced to lower terms or to decimals, independently of the other. Since the ratio of gametes derived from the dominants to those derived from the recessives is diverse in the two sets, after reduction Σ and σ may have diverse values, as may also T and τ .

(35) *Proportions of the different types of zygotes obtained from the dominants; linkage alike in both sets of gametes*

To obtain the proportions of the different classes of zygotes of generation $n + 1$, given by the mating of the gametes from the dominants of generation n , we employ directly the formulae of table 7, using of course the values of p, q, s, t obtained from table 15. To obtain correctly the final values for assortative mating it is necessary to first obtain these zygotic proportions in the forms of fractions. For this, we must divide the number in each class of zygotes by the total number of zygotes produced. This total number produced is, according to table 7, $(p+q+s+t)^2$. Furthermore, by table 15,

$$p+q+s+t = (2r+2)(c+d+g+h+i+j+k)$$

(When the letters c, d , etc., are the proportions for generation n).

Now, from this, according to table 24,

$$p+q+s+t = 2(r+1)D$$

Whence

$$(p+q+s+t)^2 = 4(r+1)^2 D^2$$

So, to obtain the zygotic proportions in the form of fractions, we must divide each value of table 7 by this expression $4(r+1)^2 D^2$. Thus, for example:

$$ABAB = \frac{p^2}{4(r+1)^2 D^2}$$

and similarly for all the 10 classes of zygotes of table 7.

Having obtained thus the relative proportions of the different types of zygotes derived from the dominant parents, we desire to know what proportions these are of the total resulting population (derived from *both* dominant and recessive parents). Now according to table 24, the dominant parents formed the fraction D/N of all parents; their progeny will therefore form D/N of all progeny, and to obtain the proportions of the entire population formed by the various classes of these progeny, we must multiply each of these proportions by D/N . The result of this will be clear from an example. As we saw in the last paragraph, the proportion for $ABAB$ before this operation is $p^2/4(r+1)^2 D^2$; multiplying this by D/N we obtain:

$$ABAB = \frac{p^2}{4(r+1)^2 DN}$$

Similarly, the proportions of the total population for all the ten types of zygotes derived from the dominants will be the values given in table 7, each divided by $4(r+1)^2DN$.

(36) *Proportions of the progeny (generation $n+1$) derived from the recessives (linkage either the same in both sets or complete in one set)*

To obtain the proportions of the various types of zygotes of the next generation ($n+1$) derived from the recessives of generation n , we proceed in a manner parallel to that employed for the dominants (35). We first obtain the gametic proportion σ and τ and if needed, Σ and T from table 25. Then the proportions of the different classes of zygotes may be obtained from table 23, if we use σ and τ or Σ and T in place of s and t .

To obtain the proportions in the form of fractions, we must divide the numbers representing each class of zygotes by the total number of zygotes. By table 23 the total number of zygotes produced is $(\sigma+\tau)^2$, or $(\sigma+\tau)(\Sigma+T)$ if linkage is complete in one set, the two expressions being equivalent. By table 25,

$$\sigma+\tau=\Sigma+T=2(c+f+l),$$

and by table 24, $2(c+f+l)$ is equivalent to $2R$. Therefore the total number of zygotes produced, $(\sigma+\tau)^2$ or $(\sigma+\tau)(\Sigma+T)$ is equal to $4R^2$.

We must therefore divide each of the zygotic values in table 23 by $4R^2$. This gives the proportions that each of the classes of zygotes are of the total zygotes produced by the recessives.

To obtain in fractional form the proportions that these are of the population as a whole (derived from both dominants and recessives), we must multiply these fractions thus far obtained by the fraction that their recessive parents are of all parents; that is, by R/N . This gives the following:

Linkage r in both sexes	Linkage complete in one sex
$c(=aBaB) = \frac{\sigma^2}{4RN}$	$\frac{\Sigma\sigma}{4RN}$
$f(=abab) = \frac{\tau^2}{4RN}$	$\frac{T\tau}{4RN}$
$l(=abaB) = \frac{2\sigma\tau}{4RN}$	$\frac{\Sigma\tau+\sigma T}{4RN}$

Thus from the recessive parents of generation n we obtain only three sorts of zygotes of generation $n+1$, in the proportions just given.

(37) To obtain now the proportions of the population in generation $n+1$ that are formed by each of the ten possible sorts of zygotes, we must simply add the proportions derived from the dominants to those from the recessives. But only the three classes of zygotes last dealt with (c , f and l) require an addition from the recessives, the others being derived entirely from the dominants. Thus the proportion of

$$c(=ABAB) \text{ is } \frac{p^2}{4(r+1)^2DN}, \text{ while that of } f(=abab) \text{ is } \frac{t^2}{4(r+1)^2DN} + \frac{r^2}{4RN}.$$

Now to free our proportions from the fractional form, we must reduce them all to a common denominator. This common denominator will evidently be $4(r+1)^2RDN$. We therefore reduce all the fractions to this denominator, and conserve merely the numerators as our proportions. This gives the results shown in table 26 (column 1). These proportions can of course be at once reduced to the fractional form by dividing each by $4(r+1)^2RDN$.

(It will be observed that the only reason for the appearance of R in the values is the occurrence of R in the denominators of the table given in section (36). If we began with a population in which there were no recessives (if for example the parents were all $ABab$), then for that generation the fractions shown in the table of section (36) would not occur, and as a result no R would appear in the values of table 26. Thus if there are no recessives in generation n ($R=0$), we do not give R the value 0 in table 26, but merely omit it entirely. If R be given the value 0 correct results will not be obtained.)

For R , D , and N only proportional values are required; thus if the values are $R=217$, $D=434$, $N=651$, we may employ simply $R=1$, $D=2$, $N=3$, since these are the proportional values.

(38) *Assortative mating; linkage complete in one sex; general formula*

When linkage is complete in one of the sets of gametes the results are to be worked out on the same principles as in the last case (32) to (37), save that for the proportions of the population produced by the dominants, we employ for the gametes both columns of table 15, followed for the zygotes by table 8. Then to obtain in fractional form the proportions from the dominants, we divide by the total number of zygotes produced from the dominants, which by table 8 is $(P+Q+S+T)(p+q+s+t)$. But by table 15

$$p+q+s+t = (2r+2)(c+d+g+h+i+j+k) = (2r+2)D \quad (\text{table 24})$$

$$P+Q+S+T = 2(c+d+g+h+i+j+k) = 2D \quad (\text{table 24})$$

Hence $(P+Q+S+T)(p+q+s+t) = 4(r+1)D^2$, which is the total number of zygotes produced by the dominants. We therefore divide each value in table 8 by $4(r+1)D^2$, obtaining thus the fractional proportions for the different zygotes obtained from the dominants. To determine what proportions these are of the entire population, we must, as in section (35), multiply each of these proportions by D/N . The general upshot of this division by $4(r+1)D^2$ and multiplication by D/N will be to divide each value in table 8 by $4(r+1)DN$. The proportions from the recessives will be as set forth in (36).

Next, as in (37), we reduce all the fractions to a common denominator, which in this case will be $4(r+1)RDN$. This enables us to discard the denominator, employing as the proportions of the different kinds of zygotes only their numerators. The results are given in the last column of table 26.

(39) Thus in assortative mating, to determine the proportions of the different classes of zygotes of the next generation $n+1$, when those of generation n are known, the order of procedure is as follows:

Give the proper values for the parents (generation n), to the letters c to l in table 1, and classify these parents into dominant D and recessive R , in accordance with table 24; find the proportional values of D , R , and N (of that table). These proportional values of R , D and N may be reduced or altered in any way that is convenient, provided the proportionality is maintained.

Obtain from the dominants the proportions of the different sets of gametes produced, by table 15. Thus the values of p , q , s and t are obtained; also (if required) of P , Q , S and T .

Obtain by table 25 the corresponding gametic proportions from the recessives, thus getting the values of σ and τ (and if required, of Σ and T).

Then, employing these gametic values, the proportions of the different classes of zygotes in generation $n+1$ are those shown in table 26.

By repetition of the procedure, the proportions for succeeding generations are obtainable.

See the example, section (42).

(40) *Derivation of the gametic proportions for the gametes produced by generation $n+1$, when those produced by n are known; assortative mating*

When we desire to obtain the zygotic proportions only for some later generation, we may shorten the procedure by working for the intervening generations only with the gametic proportions, by methods analogous to those for random mating, (12), (13) and (14), and selection of dominants (24) and (25). For this purpose we employ the values given in table 26 for the different sorts of zygotes; then determine the proportions of the different sorts of gametes produced by each,—employing in general the methods of (12), but remembering that the gametes from zygotes c , f and l are to be classified as σ and τ (or Σ and T).

The results are given in tables 27 and 28. In the repeated use of these tables, the values for D and R of the next generation ($n+1$) are to be found by the following equations (given in those tables):

$$p+q+s+t = (r+1)D, \text{ of generation } n+1$$

$$P+Q+S+T = D, \text{ of generation } n+1$$

$$\sigma+\tau \text{ (or } \Sigma+T) = R, \text{ of generation } n+1$$

Then these values of R and D are of course to be employed in the equations for finding the gametic proportions of the next generation (see the example, section 42). Only the relative values of R and D are required; if $D=99$ and $R=33$, we may use $D=3$, $R=1$.

To find for any generation the zygotic proportions, we of course employ the results of tables 27 and 28 in table 26.

(41) *The proportions for the single factor-pairs taken separately*

One of the chief points of interest is the effect of assortative mating with respect to one pair, on the proportions of another pair linked with the former. If we mate assortatively with respect to A and a , what are the results on the proportions of the pair B and b , which are linked with A and a ?

The formulae already given include all that is required for answering this question; we require merely to add together the proportions of the different zygotes that show a common constitution with respect to one of the factor pairs. For example, it is clear that $ABAB$, $AbAb$, and $ABAb$ are all to be classified as AA , when only the pair A and a is considered. It will be well to give the formulae obtained in this way from table 26, for each pair taken separately. In table 26 it will be

observed that with respect to the pair A and a , the zygotes c , d and i are AA ; g , h , j and k are Aa , while e , f and l are aa . With respect to B and b the zygotes c , e and j are BB ; g , h , i and l are Bb , while d , f and k are bb . Adding the proportions accordingly, we obtain for the proportions of the single factor-pairs taken separately the values given in table 29.

For the pair A , a , table 29 will be found to give the same values as the formulae of section (15) of my former paper (JENNINGS 1916).

(42) *Example to illustrate the use of the tables for assortative mating*

Suppose that a population consists in generation 1 of 2 $ABAB$ + 1 $AbAb$ + 2 $aBaB$ + 1 $abab$ + 4 $ABab$ + 3 $AbaB$ + 1 $ABAb$ + 2 $ABaB$ + 3 $abaB$. The linkage ratio is 2 ($r=2$), and there is assortative mating with respect to A and a .

Here, from tables 1 and 24, dominants D are:

$$c = 2; d = 1; g = 4; h = 3; i = 1; j = 2; k = 0; \text{ so that } D = 13$$

The recessives R are:

$$e = 2; f = 1; l = 3; \text{ so that } R = 6$$

Then from the dominants D , by table 15:

$$\begin{array}{ll} p = 3(4+1+2) + 4.2 + 3 = 32 & P = 11 \\ q = 3(2+1+0) + 3.2 + 4 = 19 & Q = 6 \\ s = 3.2 + 3.2 + 4 = 16 & S = 5 \\ t = 3.0 + 4.2 + 3 = 11 & T = 4 \\ p+q+s+t = (2r+2)D = 78 & P+Q+S+T = 2D = 26 \end{array}$$

From the recessives R , by table 25:

$$\begin{array}{ll} \sigma = 2.2 + 3 = 7 & \Sigma = 7 \\ \tau = 2.1 + 3 = 5 & T = 5 \\ \sigma + \tau = 2R = 12 & \Sigma + T = 2R = 12 \end{array}$$

Having thus the gametes from generation 1, we may from them find either the gametes from the next generation (2), by tables 27 and 28; or we may find at once the zygotic constitution of generation 2, by table 26. Both will be illustrated.

Gametic proportions for succeeding generations.—We shall first find the gametic proportions for the gametes derived from generation 2. Assume first that the linkage is the same ($r=2$) in both sets of gametes. Then by table 27 (remembering that R is 6 and D is 13).

$$p = 6.3.32.67 + 6(2.32.11 + 19.16) = 44640 = .3796$$

$$q = 6.3.19.62 + 6(2.19.16 + 32.11) = 26964 = .2772$$

$$s = 6(3.32.16 + 2.19.16 + 32.11) = 14976 = .1273$$

$$t = 6(3.19.11 + 2.32.11 + 19.16) = 9810 = .0834$$

$$p+q+s+t = 96390 = .8675$$

$$\text{Therefore } D = \frac{96390}{3} = 32130$$

$$\sigma = 6.16.27 + 13.3^2.7.12 = 12420 = .1056$$

$$\tau = 6.11.27 + 13.3^2.5.12 = 8802 = .0748$$

$$\sigma + \tau = 21222 = .1804$$

$$\text{Therefore } R = 21222$$

$$\text{Total gametes} = 117612 = 1.0000$$

If we desire we may reduce R and D in such a way as to make $R = 1$; that is, if we divide both by the value of R , we obtain: $R = 1$; $D = 1.513$.

Having found the proportions of the different sorts of gametes derived from generation 2, as well as R and D , for generation 2, we may now employ these values (either the entire numbers or the decimals) in finding anew the gametic proportions from generation 3, and the proportions of recessives and dominants in that generation. These may then be employed anew to find the proportions for generation 4, etc., until we reach the generation for which we wish to find the zygotic proportions.

If we assume that linkage is complete in one sex, we shall, for determining the proportions of the gametes derived from generation 2, employ table 28 in place of table 27 (used above). It is not necessary to represent the operations in detail; they will give us the following values for the proportions from the second generation:

Set 1

$$p = 30072$$

$$q = 17664$$

$$s = 9834$$

$$t = 6690$$

$$p+q+s+t = 64260 = 3D \therefore D = 21420$$

$$\sigma = 8226$$

$$\tau = 5922$$

$$\sigma + \tau = 14148 = R$$

$$\text{Total in set 1} = 7840$$

Set 2

$$P = 10140$$

$$Q = 5772$$

$$S = 3162$$

$$T = 2346$$

$$P+Q+S+T = 21420 = D$$

$$\Sigma = 8226$$

$$T = 5922$$

$$\Sigma + T = 14148 = R$$

$$\text{Total in set 2} = 35568$$

If $R = 1$, $D = 1.513$ (in generation 2).

The proportions in either or both sets may be reduced to smaller numbers by dividing all of the set by any number. It is not necessary that both sets should be divided by the same number. Thus set 1 may be reduced to decimals by dividing by the sum of the total for its set; set 2 by the total for that set.

Using these values (reduced or not), we may now find the proportions of the gametes from generation 3, and so on.

Zygotic proportions in any generation. By table 26 we may find the proportions of the different kinds of zygotes in generation 2 or 3, employing the gametic proportions already determined. As an illustration we will find these for generation 2 (employing the gametic values from generation 1 as given on page 131).

Linkage the same in both sets	Linkage complete in one set
$c (=ABAB) = 6.32^2 = 6144 = .1151$	$6.32.11 = 2112 = .1187$
$d (=AbAb) = 6.19^2 = 2166 = .0406$	$6.19.6 = 684 = .0384$
$e (=aBaB) = 6.16^2 + 13.3^2.7^2 = 7269 = .1362$	$6.5.16 + 13.3.7.7 = 2391 = .1344$
$f (=abab) = 6.11^2 + 13.3^2.5^2 = 3651 = .0684$	$6.4.11 + 13.3.5.5 = 1239 = .0697$
$g (=ABab) = 6.2.32.11 = 4224 = .0792$	$6 (11.11 + 32.4) = 1494 = .0840$
$h (=AbaB) = 6.2.19.16 = 3648 = .0684$	$6 (6.16 + 19.5) = 1146 = .0707$
$i (=ABAb) = 6.2.32.16 = 7206 = .1367$	$6 (11.19 + 32.6) = 2406 = .1353$
$j (=ABA b) = 6.2.32.16 = 6144 = .1151$	$6 (11.16 + 32.5) = 2016 = .1133$
$k (=abAb) = 6.2.19.11 = 2508 = .0470$	$6 (6.11 + 19.4) = 852 = .0479$
$l (=abaB) = 6.2.16.11 + 13.3^2.2.7.5 = 10302 = .1931$	$6 (5.11 + 16.4) + 13.3. (7.5 + 7.5) = 3444 = .1931$
Total = $4.3^2.6.13.19 = 53352 = 1.000$	Total = $4.3.6.13.9 = 17784 = 1.000$

Effect on the single factor-pairs taken separately. In generation 2, by table 29:

Linkage r in both sets	Linkage complete in one set
$AA = 6.51^2 = 15606 = .2925$	$6.17.51 = 5202 = .2925$
$Aa = 2.6.51.27 = 16524 = .3097$	$6.17.27 + 6.51.9 = 5508 = .3097$
$aa = 6.27^2 + 3^2.13.12^2 = 21222 = .3977$	$6.9.27 + 3.13.12.12 = 7074 = .3977$
Total = $6.78^2 + 3^2.13.12^2 = 53352 = 1.000$	Total = $17784 = 1.000$
$BB = 6.48^2 + 3^2.13.7^2 = 19557 = .3666$	$6.16.48 + 3.13.49 = 6519 = .3664$
$Bb = 2.6.48.30 + 2.3^2.13.7.5 = 25470 = .4774$	$6.16.30 + 6.48.10 + 3.13.70 = 8490 = .4774$
$bb = 6.30^2 + 3^2.13.5^2 = 8325 = .1560$	$6.10.30 + 3.13.25 = 2775 = .1560$
Total = $53352 = 1.000$	Total = $17784 = 1.000$

It will be observed that after this single assortative mating the proportions of BB , Bb and bb are the same whether the linkage is alike in both sets or is complete in one set; they would likewise be the same whatever the linkage, or if there were no linkage. But in later generations the proportions are diverse for different linkages, and depending on whether linkage is the same in both sets or complete in one set.

V. SELF-FERTILIZATION

Thus far we have mainly used the proportions of the different types of gametes as our units, determining from these the proportions of the different sorts of zygotes, in accordance with the principle that the random mating of any set of zygotes gives the same results as the random mating of the gametes they produce. Self-fertilization differs so greatly from random mating that it is no longer convenient to base the work on this principle; we therefore deal directly with the zygotes, obtaining formulae by means of which from the zygotic proportions in earlier generations we can determine those in later generations.

In self-fertilization the linkage ratio r would perhaps be the same for both the sets of gametes produced by the single self-fertilizing individual. It is conceivable however that linkage might be found complete in the formation of one of the two sorts of gametes. We shall therefore deal, as usual, with both cases.

(43) GENERAL FORMULA FOR DETERMINING THE ZYGOTIC PROPORTIONS IN GENERATION $n+1$, WHEN THOSE FOR GENERATION n ARE KNOWN

The population at the beginning is that shown in table 1 (proper values being given to the letter's c to l). These produce the gametes shown in table 3. Next the gametes produced by any single zygote mate together at random; those of column 1, table 3, in the case where linkage is the same in both sets of gametes; those of column 1 with those of column 2 (table 3), where linkage is complete in one set of gametes.

By making these matings; determining the zygotes produced (for generation $n+1$), then collecting the proportions of each kind of zygote of generation $n+1$, we obtain the formulae of table 30, giving directly the proportions of the zygotes of generation $n+1$ in terms of those of generation n . Column 1 gives the results when linkage is the same in both sets of gametes; column 2 the results when linkage is complete in one set.

Example. Let us take the example given in section (10), supposing however that breeding is by self-fertilization. That is, we begin with a population consisting of 3 *ABAB* + 1 *abab* + 1 *AbaB* + 4 *ABaB*; the linkage ratio r being 2. Then by table 1:

$$c = 3 \qquad f = 1 \qquad h = 1 \qquad j = 4$$

By table 30 the population in the next generation will be the following:

If linkage is the same in both sets	If linkage is complete in one set of gametes
<i>ABAB</i> = $3^2 \cdot (12+4) + 1 = 145 = .448$	$3 (12+4) = 48 = .444$
<i>AbAb</i> = $2^2 \cdot 1 = 4 = .012$	$2 \cdot 1 = 2 = .019$
<i>aBaB</i> = $3^2 \cdot 4 + 2^2 \cdot 1 = 40 = .123$	$3 \cdot 4 + 2 = 14 = .130$
<i>abab</i> = $3^2 \cdot 4 + 1 = 37 = .114$	$3 \cdot 4 = 12 = .111$
Homozygotes = 226 = .698	= 76 = .704
<i>ABab</i> = $2 \cdot 1 = 2 = .006$	= 0 = .000
<i>AbaB</i> = $2 \cdot 4 = 8 = .025$	$4 \cdot 1 = 4 = .037$
Heterozygotes = 10 = .031	= 4 = .037
<i>ABAb</i> = $4 \cdot 1 = 4 = .012$	= 1 = .000
<i>ABaB</i> = $2 \cdot 3^2 \cdot 4 + 4 \cdot 1 = 76 = .235$	$2 \cdot 3 \cdot 4 + 1 = 25 = .231$
<i>abAb</i> = $4 \cdot 1 = 4 = .012$	= 1 = .000
<i>abaB</i> = $4 \cdot 1 = 4 = .012$	= 1 = .000
Mixed = 88 = .272	= 28 = .259
Totals = 324 = 1.000	= 108 = 1.000

By substituting anew the values here found for the letters c to l in table 1, and reapplying the formulae of table 30, we can find if desired the proportions in generation $n + 2$, and so on for later generations. Either the actual numbers, or the proportions as reduced to decimals (the last column in each case, above) may be used for the further computations.

(44) *Special formulæ for the case in which the original parents are ABab*

In this specially important case, where at the beginning of self-fertilization the parents are the result of a cross between two individuals (*ABAB* and *abab*) differing in two pairs of characters, we shall develop formulae for obtaining at once the proportions of the different sorts of zygotes after any number n of self-fertilizations.

Since we begin with *ABab*, the population is represented merely by $g = 1$ (of table 1, while all the other proportions c to l of table 1 are 0). Employing table 30 we find that after one self-fertilization ($n = 1$), the different classes of zygotes are represented as follows:

Zygotes of $n = 1$	Column 1, linkage the same ($=r$) in both sets of gametes	Column 2, linkage complete in one of the sets of gametes
$c (= ABAB)$	r^2	r
$d (= AbAb)$	1	0
$e (= aBaB)$	1	0
$f (= abab)$	r^2	r
Total homozygotes	$2r^2 + 2$	$2r$
$g (= ABab)$	$2r^2$	$2r$
$h (= AbaB)$	2	0
Total heterozygotes	$2r^2 + 2$	$2r$
$i (= ABAb)$	$2r$	1
$j (= ABaB)$	$2r$	1
$k (= abAb)$	$2r$	1
$l (= abaB)$	$2r$	1
Total mixed	$8r$	4
Grand total	$4(r+1)^2$	$4(r+1)$

Now, as we work out the proportions in later generations, we find that certain relations of equality shown in the above list hold for all generations. The four kinds of homozygotes are divisible into two pairs, those retaining the linkage of the parents (that is, c and f , or $ABAB$ and $abab$); and those not retaining the original linkage (that is d and e , or $AbAb$ and $aBaB$). The two former are always equal, and so are the two latter; that is, $c = f$, and $d = e$. Furthermore, the four kinds of mixed are always present in equal proportions. The two sorts of heterozygotes, g and h , differ in their proportional values. These relations simplify the problem, since they enable us to reduce our number of unknown quantities. Thus, instead of dealing separately with the four classes of mixed, we may find merely the total proportion of mixed (which we may call M), and we can then know that the proportion for any particular sort (as $ABaB$) will be $\frac{1}{4}$ that of M . Similar relations hold for the two sorts of homozygotes in each of the pairs. The result is that there are just five diverse quantities to deal with; the two sorts of homozygotes; the corresponding two sorts of heterozygotes, and the mixed.

In our list of the proportions of the different kinds of zygotes of generation 1 just given, each proportion is of course essentially a fraction, and its actual value is obtained by dividing the value given by the total for all; that is, by $4(r+1)^2$ in column 1, or by $4(r+1)$ in column 2. Thus in column 1 the actual fractional proportion for $g(=ABab)$ is $2r^2/4(r+1)^2$, for h it is $2/4(r+1)^2$, etc. Now,

it turns out to be most convenient to deal with certain of these proportions explicitly as fractions. The same fractions found in generation 1 occur in later generations, and it is best to designate certain of the important fractions by single letters. The fractions given by the heterozygotes turn out to be of special importance, and in particular a designation is required for the fraction given by the sum of the two sorts of heterozygotes ($g+h$) and that given by their difference ($g-h$). Where linkage is complete in one set, however (column 2) $g+h$ and $g-h$ are the same, since h is zero; in this case therefore we require but one designation. In column 1 (linkage = r in both sets) we shall call the sum of $g+h$ by the letter v , the difference ($g-h$) by the letter w . In column 2 (linkage complete in one set) we shall call the sum $g+h$ by the letter u ; the difference $g-h$ is likewise u . That is, from the table on page 136.

Linkage = r in both sets	Linkage complete in one set
$v = \frac{r^2+1}{2(r+1)^2}$	$u = \frac{r}{2(r+1)}$
$w = \frac{r^2-1}{2(r+1)^2}$	

It is important to bear in mind the facts (1) that v , w and u are *fractions*; (2) that their values do not change from generation to generation, but are always those just given. It will be observed that the values for the different sorts of zygotes after one self-fertilization, as given on page 136, can be given in terms of these fractions, thus:

	Column 1	Column 2
$c = f =$	$\frac{v+w}{4}$	$\frac{u}{2}$
$d = e =$	$\frac{v-w}{4}$	0
Homozygotes =	v	u
$g =$	$\frac{v+w}{2}$	u
$h =$	$\frac{v-w}{2}$	0
Heterozygotes =	v	u
$i = j = k = l =$	$\frac{1-2v}{4}$	$\frac{1-2u}{4}$
Mixed =	$1-2v$	$1-2u$

(The values for the mixed result merely from the fact that they are equal to the total, minus the sum of the heterozygotes and homozygotes.)

If now we work out by table 30 the proportions of the different sorts of zygotes in later generations, and express our results in terms of the fractions v , w , and u , we discover for any generation n the following general relations:

	Linkage = r in both sets	Linkage complete in one set
Sum of the two classes of homozygotes, $(c+f) + (d+e)$	$\frac{2^{n-2}}{2^n} + v^n$	$\frac{2^{n-2}}{2^n} + u^n$
Difference of the two classes of homozygotes, $(c+f) - (d+e)$	$= v^1 + v^2 + v^3 \dots v^n$	$u^1 + u^2 + u^3 \dots u^n$
Sum of the two classes of heterozygotes, $g+h$	$= v^n$	u^n
Difference of the two classes of heterozygotes, $g-h$	$= w^n$	u^n

These equations may readily be solved for the values of $c+f$ and of $d+e$; also for the values of g and h . Since we know that $c=f$ and $d=e$, this will give us at once the values of c , d , e , f , g and h . We can, of course, then readily obtain the value of the total mixed (since these constitute merely the remainder) and of any particular class of mixed (since the four classes of mixed are equal). Carrying out these solutions, we obtain the final formulae set forth in table 31.

Example. Let us suppose that, beginning with the parent $ABab$, there have been three self-fertilizations; that the linkage ratio is 2; and that linkage is the same in both sets of gametes.

Here we have:

$$r = 2 \quad v = \frac{5}{18} \quad u = \frac{8}{18} \quad n = 3$$

Hence:

$$\text{Total homozygotes} = \frac{2^2 - 1}{2^2} + \left(\frac{5}{18}\right)^3 = \frac{3}{4} + \frac{125}{5832} = \frac{4489}{5832} = .7714$$

$$c(=ABAB) = \frac{2^2 - 1}{2^4} + \frac{1}{4} \left[\left(\frac{5}{18}\right)^3 + \left(\frac{8}{18}\right)^3 + \left(\frac{8}{18}\right)^2 + \frac{8}{18} \right] = \frac{1415}{5832} = .2427$$

$$d(=AbAb) = \frac{2^2 - 1}{2^4} + \frac{1}{4} \left[\left(\frac{5}{18}\right)^3 - \left(\frac{8}{18}\right)^3 - \left(\frac{8}{18}\right)^2 - \frac{8}{18} \right] = \frac{1869}{11664} = .1603$$

$$e(=aRaB) = .1431$$

$$f(=abab) = .2427$$

$$\text{Total heterozygotes} = \left(\frac{5}{18}\right)^3 = \frac{125}{5832} = .0214$$

$$g(=ABab) = \frac{1}{2} \left[\left(\frac{5}{18}\right)^3 + \left(\frac{8}{18}\right)^3 \right] = \frac{76}{5832} = .0130$$

$$h(=AbAb) = \frac{1}{2} \left[\left(\frac{5}{18}\right)^3 - \left(\frac{8}{18}\right)^3 \right] = \frac{49}{5832} = .0084$$

$$\text{Total mixed} = \frac{1}{4} - 2\left(\frac{5}{18}\right)^3 = \frac{1399}{5832} = .2382$$

$$\text{Any single class of mixed (as } ABAb) = \frac{1}{4} \times \frac{1399}{5832} = .0591$$

If we assume that linkage is complete in one of the sets of gametes, we have $u = \frac{1}{3}$; the results are then obtained in a similar manner; they are as follows:

$$\text{Total homozygotes} = .7870$$

$$d = e = .0764$$

$$c = f = .3171$$

$$\text{Total heterozygotes} = (1/3)^3 = 1/27 = .0370$$

$$g(=ABab) = (1/3)^3 = .0370$$

$$c = f = .3171$$

$$\text{Total mixed} = 1/2^2 - 2(1/3)^3 = 38/216 = .1759$$

$$\text{Any single class of mixed, as } ABaB = (1/2)^4 - 1/2(1/3)^3 = .0439$$

If we classify the results with respect to either of the single pairs of factors (as A and a), we of course obtain the same results given in section (25) of my previous paper (JENNINGS 1916), that is:

$$AA \text{ (or } BB) = \frac{2^n - 1}{2^{n+1}}$$

$$aa \text{ (or } bb) = \frac{2^n - 1}{2^{n+1}}$$

$$Aa \text{ (or } Bb) = \frac{1}{2^n}$$

(45) *Parents AbaB (derived from a cross of AbAb with aBaB)*

In this case, the results are as given in table 31, but with the following alterations in the formulae:

The values for c and d are to be interchanged.

The values for e and f are to be interchanged.

The values for g and h are to be interchanged.

The values remain unchanged for the total homozygotes; for the total heterozygotes; for the total mixed; and for any particular class of mixed.

REMARKS ON INBREEDING. To obtain a general formula for inbreeding with brother by sister mating, when two linked pairs of characters are considered, one begins with a family composed as in table 1, proper values being given to the letters c to l . When such a family is inbred, the linkage ratio being r for both sexes, it gives 55 diverse types of

families (the number of families being $\frac{n(n+1)}{2}$ where n is the number

of differing individuals in the original family). By determining the types of families produced from each of these 55 families, and collecting the results for each of the possible 55 kinds of newly formed families, one obtains formulae giving the constitution in families in the generation $n + 1$, when that in generation n is known. Such formulae are complex, some of the 55 equations being made up of as many as 24 terms. It hardly seems worth while to publish the complex table of formulae thus obtained; possibly it may be employed later to obtain the actual gametic constitution of the population in later generations for the more important special cases, as when the original parents are all *ABab*, and the like. The entire subject of inbreeding with relation to two pairs of linked factors is therefore reserved for further treatment. The paper of DETLEFSEN (1914) contains discussions and formulae for certain special cases of inbreeding when two pairs of independent factors are dealt with. The present writer would find it a relief if some one else would deal thoroughly with the laborious problem of the effects of inbreeding on two pairs of linked factors.

SUMMARY

This paper derives formulae for finding in later generations the results of continued breeding by a given system, when two pairs of characters, linked or independent, are considered. Its primary purpose is to render it possible to determine the effects of linkage on the distribution of the factors. The systems of breeding considered are: random mating; selection with respect to a given single character; assortative mating with respect to a single character; and self-fertilization. In each system two cases are dealt with; that in which linkage is the same in both sets of gametes; and that in which linkage is complete in one set. In each system general formulae are derived for transforming generation n into generation $n + 1$. In several systems special formulae are given for finding directly in any later generation n the proportions of the population, when one begins with parents that are a cross between *ABAB* and *abab*; or between *AbAb* and *aBaB*. With regard to selection and assortative mating with respect to a single character, formulae are given for the effect on the single pairs taken separately; thus for the effect of selection or assortative mating with respect to one character on the distribution of another character linked with that one.

The formulae are collected for convenience in 31 tables, which are placed in order at the end of the paper.

LITERATURE CITED

- DETLEFSEN, J. A., 1914 Genetic studies on a cavy species cross. Carnegie Institution of Washington, Publication No. 205, 134 pp.
- JENNINGS, H. S., 1916 The numerical results of diverse systems of breeding. *Genetics* 1: 53-89.
- WENTWORTH, E. N., and REMICK, B. L., 1916 Some breeding properties of the generalized Mendelian population. *Genetics* 1: 608-616.

TABLES FOR USE IN COMPUTING THE NUMERICAL RESULTS OF DIVERSE
SYSTEMS OF BREEDING, WITH RESPECT TO TWO PAIRS OF FACTORS

Table 1. The ten diverse possible classes of zygotes with respect to two pairs of factors (A, a and B, b), with the algebraic designations (c to l) that will be employed to represent their respective proportions.

By giving the proper values to the letters c to l , any population may be represented by this table.

<i>Homozygotes</i>	<i>Heterozygotes</i>	<i>Mixed</i>
$c.ABAB$	$g.ABab$	$i.ABAb$
$d.AbAb$	$h.AbaB$	$j.ABaB$
$e.aBaB$		$k.abAb$
$f.abab$		$l.abaB$

With respect to the single pairs taken separately:

$$\begin{array}{lll}
 AA = c + d + i & aa = e + f + l & Aa = g + h + j + k \\
 BB = c + e + j & bb = d + f + k & Bb = g + h + i + l
 \end{array}$$

Table 2. The four possible classes of gametes with respect to two pairs of factors, with the algebraic designations (p, q, s, t) for their relative proportions.

$p.AB$	$q.Ab$	$s.aB$	$t.ab$
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(To distinguish certain classes of gametes, in some cases the capital letters, P, Q, S, T , will be used in place of the lower case letters; and in assortative mating, for special purposes the corresponding Greek letters σ and τ will be used for s and t . See tables 5, 8, 25, 26, etc.)

Table 3. Gametes given by the ten sorts of zygotes of table 1, when the linkage is r ; and when linkage is complete.

Zygotes	Gametes produced	
	1. Linkage = r	2. Linkage complete
$c.ABAB$	$c.(2r+2)AB$	$2c.AB$
$d.AbAb$	$d.(2r+2)Ab$	$2d.Ab$
$e.aBaB$	$e.(2r+2)aB$	$2e.aB$
$f.abab$	$f.(2r+2)ab$	$2f.ab$
$g.ABab$	$g.(r.AB+1.Ab+1.aB+r.ab)$	$g.AB+g.ab$
$h.AbaB$	$h.(r.Ab+1.AB+1.ab+r.aB)$	$h.Ab+h.aB$
$i.ABAb$	$i.(r+1)AB+i.(r+1)Ab$	$i.AB+i.Ab$
$j.ABaB$	$j.(r+1)AB+j.(r+1)aB$	$j.AB+j.aB$
$k.abAb$	$k.(r+1)ab+k.(r+1)Ab$	$k.ab+k.Ab$
$l.abab$	$l.(r+1)ab+l.(r+1)aB$	$l.ab+l.aB$

Table 4. Linkage r . Proportions of the different kinds of gametes produced by a population of zygotes (of table 1) in terms of the proportions of the zygotes.

$$\begin{aligned}
 p(=AB) &= (r+1)(2c+i+j)+rg+h \\
 q(=Ab) &= (r+1)(2d+i+k)+rh+g \\
 s(=aB) &= (r+1)(2e+j+l)+rh+g \\
 t(=ab) &= (r+1)(2f+k+l)+rg+h \\
 p+q+s+t &= (2r+2)(c+d+e+f+g+h+i+j+k+l)
 \end{aligned}$$

Table 5. Linkage complete. Proportions of the different kinds of gametes produced by a population of zygotes (table 1), in terms of the proportions of the parent zygotes.

$$\begin{aligned}
 P(=AB) &= 2c+g+i+j \\
 Q(=Ab) &= 2d+h+i+k \\
 S(=aB) &= 2e+h+j+l \\
 T(=ab) &= 2f+g+k+l \\
 P+Q+S+T &= 2(c+d+e+f+g+h+i+j+k+l) \\
 p+q+s+t \text{ (of table 4)} &= (r+1)(P+Q+S+T)
 \end{aligned}$$

Table 6. Random mating of the four types of gametes (of table 2), with the zygotes produced.

Gametes		Zygotes				
$p. AB$	} \times {	$p. AB$	$p.^2 AB$ AB	$pq. AB$ Ab	$ps. AB$ aB	$pt. AB$ ab
$q. Ab$		$q. Ab$	$qp. Ab$ AB	$q.^2 Ab$ Ab	$qs. Ab$ aB	$qt. Ab$ ab
$s. aB$		$s. aB$	$sp. aB$ AB	$sq. aB$ Ab	$s.^2 aB$ aB	$st. aB$ ab
$t. ab$		$t. ab$	$tp. ab$ AB	$tq. ab$ Ab	$ts. ab$ aB	$t.^2 ab$ ab

Table 7. Proportions of the various types of zygotes resulting from the random mating of the four types of gametes (of tables 2 and 6), in terms of the proportions of the gametes.

Homozygotes

$$c(=ABAB) = p^2$$

$$d(=AbAb) = q^2$$

$$e(=aBaB) = s^2$$

$$f(=abab) = t^2$$

Mixed

$$i(=ABAb) = 2pq$$

$$j(=ABaB) = 2ps$$

$$k(=abAb) = 2qt$$

$$l(=abaB) = 2st$$

$$\text{Total homozygotes} = p^2 + q^2 + s^2 + t^2. \quad \text{Total mixed} = 2(pq + ps + qt + st)$$

Heterozygotes

$$g(=ABab) = 2pt$$

$$h(=AbaB) = 2qs$$

$$\text{Total heterozygotes} = 2(pt + qs)$$

$$\text{Total zygotes} = (p + q + s + t)^2$$

Table 8. Proportions of the various types of zygotes resulting from the random mating of the four types of gametes produced with linkage r (table 4), with the four types produced with complete linkage (table 5).

<i>Homozygotes</i>	<i>Mixed</i>
$c(=ABAB) = Pp$	$i(=ABAb) = Pq + pQ$
$d(=AbAb) = Qq$	$j(=ABaB) = Ps + pS$
$e(=aBaB) = Ss$	$k(=abAb) = Qt + qT$
$f(=abab) = Tt$	$l(=abaB) = St + sT$
Total homozygotes $= Pp + Qq + Ss + Tt$	Total mixed $= Pq + pQ + Ps + pS + Qs + qS + Qt + qT + St + sT$
<i>Heterozygotes</i>	
$g(=ABab) = Pt + pT$	
$h(=AbaB) = Qs + qS$	
Total heterozygotes $= Pt + pT + Qs + qS$	
Total zygotes $= (P + Q + S + T)(p + q + s + t)$	

Table 9. Random mating, linkage the same ($=r$) in both sets of gametes. Formulae for the proportions of the gametes derived from generation $n + 1$ (therefore producing generation $n + 2$), in terms of the gametes derived from generation n (and therefore producing generation $n + 1$). That is, formulae for p_{n+1} , q_{n+1} , s_{n+1} , t_{n+1} , in terms of p_n , q_n , s_n , t_n .

Gametes from generation $n + 1$	In terms of gametes from generation n
$p(=AB)$	$= (r + 1)p(p + q + s) + rpt + qs$
$q(=Ab)$	$= (r + 1)q(p + q + t) + rqs + pt$
$s(=aB)$	$= (r + 1)s(p + s + t) + rqs + pt$
$t(=ab)$	$= (r + 1)t(q + s + t) + rpt + qs$
$p + q + s + t$	$= (r + 1)(p + q + s + t)^2$

Table 10. Random mating; independent factors (no linkage). Proportions of the different kinds of gametes derived from generation $n + 1$, in terms of those derived from generation n . This is table 9, simplified for the case of no linkage ($r = 1$).

Gametes from $n + 1$	In terms of gametes from n
$p(=AB)$	$= 2p(p + q + s) + pt + qs$
$q(=Ab)$	$= 2p(p + q + t) + qs + pt$
$t(=ab)$	$= 2t(q + s + t) + pt + qs$
$s(=aB)$	$= 2s(p + s + t) + qs + pt$
$p + q + s + t$	$= 2(p + q + s + t)^2$

Table 11. Random mating; linkage complete in one set of gametes, r in the other. Formulae for the proportions of the two sets of gametes derived from generation $n+1$, in terms of the gametic proportions of the two sets derived from generation n .

Gametes from $n+1$	In terms of gametes from n Set 1. Gametes with linkage r .
$p(=AB) =$	$(r+1)p(P+Q+S) + (r+1)P(p+q+s) + r(Pt+pT) + Qs+qS$
$q(=Ab) =$	$(r+1)q(P+Q+T) + (r+1)Q(p+q+t) + r(Qs+qS) + Pt+pT$
$s(=aB) =$	$(r+1)s(P+S+T) + (r+1)S(p+s+t) + r(Qs+qS) + Pt+pT$
$t(=ab) =$	$(r+1)t(Q+S+T) + (r+1)T(q+s+t) + r(Pt+pT) + Qs+qS$
$p+q+s+t =$	$2(r+1)(P+Q+S+T)(p+q+s+t)$

Set 2. Gametes with complete linkage

$$\begin{aligned}
 P(=AB) &= P(p+q+s+t) + p(P+Q+S+T) \\
 Q(=Ab) &= Q(p+q+s+t) + q(P+Q+S+T) \\
 S(=aB) &= S(p+q+s+t) + s(P+Q+S+T) \\
 T(=ab) &= T(p+q+s+t) + t(P+Q+S+T) \\
 P+Q+S+T &= 2(P+Q+S+T)(p+q+s+t)
 \end{aligned}$$

Table 12. Random mating, linkage complete in one set of gametes, r in the other set. Certain relations between the proportions of the gametes of the two sets, in any given generation. Derived from table 11.

(The same relations hold for the two sets of table 15, in selection for dominants.)

Set 1	Set 2
$p+q = (r+1)(P+Q)$	
$p+s = (r+1)(P+S)$	
$q+t = (r+1)(Q+T)$	
$s+t = (r+1)(S+T)$	
$p+q+s+t = (r+1)(P+Q+S+T)$	

Table 13. Random mating, original parents all $ABab$; linkage r in both sets of gametes. Proportions of the different classes of gametes for producing any required generation n .

Gametes for producing
generation n

$$\begin{aligned}
 p(=t) &= (r+1)^n + r^n - r^{n-1} \\
 q(=s) &= (r+1)^n - r^n + r^{n-1}
 \end{aligned}$$

If the original parents are $AbaB$, interchange the values of $p(=t)$ and $q(=s)$.

Table 14. Random mating, original parents all $ABab$; linkage r in one set of gametes, complete in the other. Proportions of the different classes of gametes for producing any required generation n .

Gametes for producing
generation n

$$\begin{aligned} p(=t) &= 2^{n-2}(r+1)^n + r^2(2r+1)^{n-2} \\ q(=s) &= 2^{n-2}(r+1)^n - r^2(2r+1)^{n-2} \\ P(=T) &= 2^{n-2}(r+1)^{n-1} + r(2r+1)^{n-2} \\ Q(=S) &= 2^{n-2}(r+1)^{n-1} - r(2r+1)^{n-2} \end{aligned}$$

If the original parents are $AbaB$, interchange the values of $p(=t)$ and $q(=s)$; also interchange the values of $P(=T)$ and $Q(=S)$.

Table 15. Selection for dominant A . Proportions of the different kinds of gametes produced by a population of zygotes (of table 1), in terms of the proportions of the zygotes; when linkage is r ; and when it is complete.

Set 1. Linkage r	Set 2. Linkage complete
$p(=AB) = (r+1)(2c+i+j) + rg+h$	$P(=AB) = 2c+g+i+j$
$q(=Ab) = (r+1)(2d+i+k) + rh+j$	$Q(=Ab) = 2d+h+i+k$
$s(=aB) = (r+1)j + rh+g$	$S(=aB) = h+j$
$t(=ab) = (r+1)k + rg+h$	$T(=ab) = g+k$
$p+q+s+t = (2r+2)(c+d+g+h+i+j+k)$	$P+Q+S+T = 2(c+d+g+h+i+j+k)$

The relations shown in table 12 hold for the two sets of table 15, as well as for those of table 11.

Table 16. Selection for dominant A ; linkage the same ($=r$) in both sets of gametes. Proportions of the different sorts of gametes derived from generation $n+1$, in terms of those derived from generation n .

Gametes produced by generation $n+1$	In terms of gametes produced by generation n
$p(=AB) =$	$(r+1)p(p+q+s) + rpt+qs$
$q(=Ab) =$	$(r+1)q(p+q+t) + rqs+pt$
$s(=aB) =$	$(r+1)ps+rqs+pt$
$t(=ab) =$	$(r+1)qt+rpt+qs$
$p+q+s+t =$	$(r+1)(p+q)(p+q+s+t)$

Table 17. Selection of dominant A ; linkage complete in one set of gametes; r in the other. Proportions of the two sets of gametes derived from generation $n + 1$, in terms of the gametic proportions of the two sets derived from generation n .

Set 1. Gametes with linkage r

Gametes from

$n + 1$

In terms of gametes from n

$$p(=AB) =$$

$$(r+1)p(P+Q+S) + (r+1)P(p+q+s) + r(Pt+pT) + Qs+qS$$

$$q(=Ab) =$$

$$(r+1)q(P+Q+T) + (r+1)Q(p+q+t) + r(Qs+qS) + Pt+pT$$

$$s(=aB) = (r+1)(Sp+sP) + r(Qs+qS) + Pt+pT$$

$$t(=ab) = (r+1)(Qt+qT) + r(Pt+pT) + Qs+qS$$

$$p+q+s+t = 2(r+1)[(p+q)(P+Q+S+T) + (P+Q)(s+t)]$$

Set 2. Gametes with complete linkage

$$P(=AB) = P(p+q+s+t) + p(P+Q+S+T)$$

$$Q(=Ab) = Q(p+q+s+t) + q(P+Q+S+T)$$

$$S(=aB) = S(p+q) + s(P+Q)$$

$$T(=ab) = T(p+q) + t(P+Q)$$

$$P+Q+S+T = 2[(p+q)(P+Q+S+T) + (P+Q)(s+t)]$$

Table 18. Proportions of the gametes containing A or a ; and of those containing B or b . (In terms of tables 9 to 11, or of tables 15 to 17; these relations of course hold equally of random mating and of selection of dominants.)

Set 1.

Gametes with linkage r

$$A = p + q$$

$$a = s + t$$

$$B = p + s$$

$$b = q + t$$

Set 2.

Gametes with complete linkage

$$A = P + Q$$

$$a = S + T$$

$$B = P + S$$

$$b = Q + T$$

Table 19. Proportions of the different classes of zygotes in generation $n + 1$, with reference to the single factor-pairs taken separately, in terms of the gametes of tables 9 to 11 or of tables 15 to 17.

Set 1. Linkage (r) the same in both sets of gametes

$$AA = (p+q)^2$$

$$Aa = 2(p+q)(s+t)$$

$$aa = (s+t)^2$$

$$BB = (p+s)^2$$

$$Bb = 2(p+s)(q+t)$$

$$bb = (q+t)^2$$

Set 2. Linkage complete in one set of gametes; r in the other

$$AA = (p+q)(P+Q)$$

$$Aa = (p+q)(S+T) + (P+Q)(s+t)$$

$$aa = (s+t)(S+T)$$

$$BB = (p+s)(P+S)$$

$$Bb = (p+s)(Q+T) + (P+S)(q+t)$$

$$bb = (q+t)(Q+T)$$

Table 20. Selection of parents containing dominant *A*. Original parents all *ABab*. Proportions of the 10 possible sorts of individuals (zygotes) produced for the first 4 generations (*n*) when there is no linkage ($r=1$), when the linkage ratio is 2 in both sexes ($r=2$), and when the linkage is 2 in one sex, but complete in the other ($r=2+$).

$n =$		$r = 1$		$r = 2$		$r = 2+$		$r = 2$		$r = 2+$	
$r = 1$		$r = 2$		$r = 2+$		$r = 2$		$r = 2$		$r = 2+$	
<i>ABAB</i>	$= 1=.0625$	$4=.1111$		$2=.1667$		$4=.1111$		$121=.1670$		$260=.2675$	
<i>ABaB</i>	$= 1=.0625$	$1=.0278$		$0=0$		$4=.1111$		$49=.0672$		$20=.2058$	
<i>aBaB</i>	$= 1=.0625$	$1=.0278$		$0=0$		$1=.0278$		$16=.0219$		$7=.0072$	
<i>abab</i>	$= 1=.0625$	$4=.1111$		$2=.1667$		$1=.0278$		$25=.0343$		$55=.0566$	
Homo.	$= 4=.2500$	$10=.2778$		$4=.3333$		$10=.2778$		$211=.2894$		$342=.3519$	
<i>ABab</i>	$= 2=.1250$	$8=.2222$		$4=.3333$		$4=.1111$		$110=.1509$		$240=.2469$	
<i>ABaB</i>	$= 2=.1250$	$2=.0555$		$0=0$		$4=.1111$		$56=.0768$		$24=.0247$	
Hetero.	$= 4=.2500$	$10=.2778$		$4=.3333$		$8=.2222$		$166=.2277$		$264=.2716$	
<i>ABAb</i>	$= 2=.1250$	$4=.1111$		$1=.0833$		$8=.2222$		$154=.2112$		$152=.1564$	
<i>ABaB</i>	$= 2=.1250$	$4=.1111$		$1=.0833$		$4=.1111$		$88=.1207$		$96=.0988$	
<i>abAB</i>	$= 2=.1250$	$4=.1111$		$1=.0833$		$4=.1111$		$70=.0960$		$72=.0741$	
<i>abab</i>	$= 2=.1250$	$4=.1111$		$1=.0833$		$2=.0555$		$40=.0549$		$46=.0473$	
Mixed	$= 8=.5000$	$16=.4444$		$4=.3333$		$18=.5000$		$352=.4829$		$366=.3765$	
Total	$= 16=1$	$36=1$		$12=1$		$36=1$		$729=1$		$972=1$	
$n =$		$r = 3$		$r = 4$		$r = 2$		$r = 2$		$r = 2+$	
$r = 1$		$r = 2$		$r = 2+$		$r = 1$		$r = 1$		$r = 2+$	
<i>ABAB</i>	$= 9=.1406$	$1024=.1975$		$1638=.3160$		$16=.1600$		$143,641=.2189$		$33,480=.3444$	
<i>ABaB</i>	$= 9=.1406$	$484=.0934$		$186=.0347$		$16=.1600$		$72,361=.1103$		$4,392=.0452$	
<i>aBaB</i>	$= 1=.0156$	$81=.0156$		$40=.0077$		$1=.0100$		$7,396=.0113$		$689=.0071$	
<i>abab</i>	$= 1=.0156$	$81=.0156$		$130=.0251$		$1=.0100$		$5,776=.0088$		$1,265=.0130$	
Homo.	$= 20=.3125$	$1670=.3221$		$1938=.3738$		$34=.3400$		$229,174=.3493$		$39,826=.4097$	
<i>ABab</i>	$= 6=.0937$	$576=.1111$		$927=.1788$		$8=.0800$		$57,608=.0878$		$13,070=.1345$	
<i>ABaB</i>	$= 6=.0937$	$396=.0764$		$171=.0330$		$8=.0800$		$46,268=.0705$		$3,494=.0359$	
Hetero.	$= 12=.1875$	$972=.1875$		$1098=.2118$		$16=.1600$		$103,876=.1583$		$16,564=.1704$	
<i>ABAb</i>	$= 18=.2813$	$1408=.2716$		$1098=.2118$		$32=.3200$		$203,902=.3107$		$24,336=.2504$	
<i>ABaB</i>	$= 6=.0937$	$576=.1111$		$531=.1024$		$8=.0800$		$65,188=.0993$		$9,754=.1003$	
<i>abAB</i>	$= 6=.0937$	$396=.0764$		$315=.0608$		$8=.0800$		$40,888=.0623$		$4,786=.0492$	
<i>abab</i>	$= 2=.0313$	$162=.0312$		$154=.0207$		$2=.0200$		$13,072=.0199$		$1,934=.0199$	
Mixed	$= 32=.5000$	$2542=.4904$		$2098=.4049$		$50=.5000$		$323,050=.4923$		$40,810=.4199$	
Total	$= 64=1$	$5184=1$		$5184=1$		$100=1$		$656,100=1$		$97,200=1$	

Table 21. Selection of parents containing dominant *A*. Original parents all *ABab*. Proportions of the different sorts of individuals for the single factor pairs taken separately, for the first four generations of selection, when there is no linkage ($r=1$); when the linkage ratio is 2 in both sexes ($r=2$), and when the linkage is 2 in one sex but complete in the other ($r=2+$). Primarily to illustrate the effect of selection with respect to one factor-pair (*A*, *a*) on another factor-pair (*B*, *b*), linked with the former, or independent of it.

<i>n</i> = 1			2		
<i>r</i> = 1	2	2+	1	2	2+
<i>AA</i> = 1	1	1	4	4	4
<i>Aa</i> = 2	2	2	4	4	4
<i>aa</i> = 1	1	1	1	1	1
Totals 4	4	4	9	9	9
<i>BB</i> = 1	1	1	1	25	121
<i>Bb</i> = 2	2	2	2	40	154
<i>bb</i> = 1	1	1	1	16	49
Totals 4	4	4	4	81	324
<i>n</i> = 3			4		
<i>r</i> = 1	2	2+	1	2	2+
<i>AA</i> = 9	9	9	16	16	16
<i>Aa</i> = 6	6	6	8	8	8
<i>aa</i> = 1	1	1	1	1	1
Totals 16	16	16	25	25	25
<i>BB</i> = 1	1681	2209	1	961	14641
<i>Ab</i> = 2	2542	2350	2	1426	14278
<i>bb</i> = 1	961	625	1	529	3481
Totals 4	5184	5184	4	2916	32400

Table 22. Selection of recessive *aa*; linkage either *r*, or complete. Proportions of the different kinds of gametes produced by a population (table 1), in terms of the proportions of the zygotes given in table 1.

$$\begin{aligned}
 s \text{ or } S(=aB) &= 2e+l \\
 t \text{ or } T(=ab) &= 2f+l \\
 s+t \text{ (or } S+T) &= 2(e+f+l)
 \end{aligned}$$

Table 23. Selection of recessive aa ; linkage either r in both sets of gametes, or complete in one set. Proportions of the different classes of zygotes, in any generation n , in terms of the gametes (table 22) from generation I.

$$\begin{aligned} e(=aBaB) &= s^2 \quad (\text{or } sS) \\ f(=abab) &= t^2 \quad (\text{or } tT) \\ l(=abaB) &= 2st \quad (\text{or } sT+St) \\ \text{Total zygotes } (e+f+l) &= (s+t)^2. \quad (\text{or } (s+t)(S+T)) \end{aligned}$$

Table 24. Assortative mating. Designations to be employed for the sums of the classes of zygotes of table I that are dominant (D) with respect to the character A ; that are recessive (R) with respect to that character; and for the sum of all (N). In terms of the proportions given in table I.

$$\begin{aligned} D &= c+d+g+h+i+j+k \\ R &= e+f+l \\ N &= D+R \end{aligned}$$

Table 25. Assortative mating. Proportions of the different kinds of gametes produced by the recessives (aa) of a population (table I), in terms of the zygotes producing them. (This table is the same as table 22, but with substitution of Greek letters for the corresponding English ones, for the exigencies of work with assortative mating.)

Set 1. Gametes formed with linkage r

$$\begin{aligned} \sigma(=aB) &= 2e+l \\ \tau(=ab) &= 2f+l \\ \sigma+\tau &= 2(e+f+l) \end{aligned}$$

Set 2. Gametes formed with complete linkage

$$\begin{aligned} \Sigma(=aB) &= 2e+l \\ \text{T}(=ab) &= 2f+l \\ \Sigma+\text{T} &= 2(e+f+l) \end{aligned}$$

Table 26. Assortative mating. Proportions of the different classes of zygotes in the next generation $n+1$, in terms of the gametes producing them (of tables 15 and 25), and of the proportions of D , R , and N of table 24.

N.B. Where R is 0, simply omit R from the values; do *not* give R the value of 0 (see note in section (37)). For R , D and N any values that conserve their correct relative proportions may be employed.

Zygotes of $n+1$	Column 1. Proportions when the linkage (r) is the same in both sets of gametes	Column 2. Proportions when the linkage is complete in one set of gametes, r in the other
$c(=ABAB)$	Rp^2	$R P p$
$d(=AbAb)$	Rq^2	$R Q q$
$c(=aBaB)$	$Rs^2+D(r+1)^2\sigma^2$	$R S s+D(r+1)\Sigma\sigma$
$f(=abab)$	$Rt^2+D(r+1)^2\tau^2$	$R T t+D(r+1)T\tau$
$g(=ABab)$	$2Rpt$	$R(Pt+pT)$
$h(=AbaB)$	$2Rqs$	$R(Qs+qS)$
$i(=ABAb)$	$2Rpq$	$R(Pq+pQ)$
$j(=ABaB)$	$2Rps$	$R(Ps+pS)$
$k(=abAb)$	$2Rqt$	$R(Qt+qT)$
$l(=abaB)$	$2Rst+2(r+1)^2D\sigma\tau$	$R(S t+s T)+D(r+1)(\Sigma\tau+\sigma T)$

Table 27. Assortative mating. Linkage (r) the same in both sets of gametes. Formulae for deriving the proportions of the different kinds of gametes produced by generation $n+1$, when the gametes produced by generation n are known.

N. B. Where R is 0 it is to be omitted from the equations; *not* given the value 0.

(1) From the dominants

Gametes from $n+1$ In terms of gametes from n , and of R and D of generation n

$$\begin{aligned}
 p(=AB) &= R(r+1)p(p+q+s)+R(rpt+qs) \\
 q(=Ab) &= R(r+1)q(p+q+t)+R(rqs+pt) \\
 s(=aB) &= R[(r+1)ps+rqs+pt] \\
 t(=ab) &= R[(r+1)qt+rpt+qs]
 \end{aligned}$$

(2) From the recessives

$$\sigma(=aB) = Rs(s+t)+D(r+1)^2\sigma(\sigma+\tau)$$

$$\tau(=ab) = Rt(s+t)+D(r+1)^2\tau(\sigma+\tau)$$

$$D_{n+1} = \frac{p+q+s+t}{r+1} \text{ of generation } n+1$$

$$R_{n+1} = \sigma+\tau \text{ of generation } n+1$$

Table 28. Assortative mating; linkage complete in one set of gametes, r in the other. Formulae for the gametes produced by generation $n+1$, in terms of those produced by generation n .

N.B. Where R is 0, the factor R is to be omitted from the equations. It must *not* be given the value 0.

Set 1. From the sex in which linkage is r .

(1) From the dominants

Gametes from

$n+1$ In terms of gametes from n , and of R and D of n

$$p(=AB) =$$

$$R(r+1)P(p+q+s) + R(r+1)p(P+Q+S) + R(rPt+rpT+Qs+qS)$$

$$q(=Ab) =$$

$$R(r+1)Q(p+q+t) + R(r+1)q(P+Q+T) + R(rQs+rqS+Pt+pT)$$

$$s(=aB) = R(r+1)(Ps+pS) + R(rQs+rqS+Pt+pT)$$

$$t(=ab) = R(r+1)(Qt+qT) + R(rPt+rpT+Qs+qS)$$

(2) From the recessives

$$\sigma(=aB) = R(2Ss+St+sT) + D(r+1)(2\Sigma\sigma+\Sigma\tau+\sigma T)$$

$$\tau(=ab) = R(2Tt+St+sT) + D(r+1)(2T\tau+\Sigma\tau+\sigma T)$$

Set 2. From the sex with linkage complete.

(1) From the dominants

$$P(=AB) = RP(p+q+s+t) + Rp(P+Q+S+T)$$

$$Q(=Ab) = RQ(p+q+s+t) + Rq(P+Q+S+T)$$

$$S(=aB) = RS(p+q) + Rs(P+Q)$$

$$T(=ab) = RT(p+q) + Rt(P+Q)$$

(2) From the recessives

$$\Sigma(=aB) = R(2Ss+St+sT) + D(r+1)(2\Sigma\sigma+\Sigma\tau+\sigma T)$$

$$T(=ab) = R(2Tt+St+sT) + D(r+1)(2T\tau+\Sigma\tau+\sigma T)$$

$$D_{n+1} = P+Q+S+T = \frac{p+q+s+t}{r+1} \text{ (of generation } n+1)$$

$$R_{n+1} = \sigma+\tau = \Sigma+T \text{ (of generation } n+1)$$

Table 29. Assortative mating. Proportions of the different classes of zygotes in generation $n + 1$, with respect to the two pairs of factors taken separately, in terms of the gametes from generation n , and of R and D of generation n . Derived from table 26.

Zygotes	Column 1. Proportions when the linkage is the same (r) in both sets of gametes.	Column 2. Proportions when the linkage is complete in one set, r in the other set of gametes.
$AA(=c+d+i)$ $Aa(=g+h+j+k)$ $aa(=e+f+l)$	$R(p+q)^2$ $2R(p+q)(s+t)$ $R(s+t)^2 + (r+1)^2 D(\sigma+\tau)^2$	$R(P+Q)(p+q)$ $R(P+Q)(s+t) + R(p+q)(S+T)$ $R(S+T)(s+t) + (r+1)D(\Sigma+T)(\sigma+\tau)$
Total	$R(p+q+s+t)^2 + (r+1)^2 D(\sigma+\tau)^2$	$R(P+Q+S+T)(p+q+s+t) + (r+1)D(\Sigma+T)(\sigma+\tau)$
$BB(=c+e+j)$ $Bb(=g+h+i+l)$	$R(p+s)^2 + (r+1)^2 D\sigma^2$ $2R(p+s)(q+t) + 2(r+1)^2 D\sigma\tau$	$R(P+S)(p+s) + (r+1)D\Sigma\sigma$ $R(P+S)(q+t) + R(p+s)(Q+T) + (r+1)D(\Sigma\tau+\sigma T)$
$bb(=d+f+k)$	$R(q+t)^2 + (r+1)^2 D\tau^2$	$R(Q+T)(q+t) + (r+1)D\tau T$
Total	$R(p+q+s+t)^2 + (r+1)^2 D(\sigma+\tau)^2$	$R(P+Q+S+T)(p+q+s+t) + (r+1)D(\Sigma+T)(\sigma+\tau)$

Table 30. Self-fertilization; proportions of the different kinds of zygotes in generation $n + 1$, in terms of their proportions in generation n (the proportions in generation n are those given in table 1). Column 1, results when linkage is the same in both sets of gametes; column 2, when linkage is complete in one set.

Zygotes of $n+1$	In terms of proportions of zygotes of generation n	
	1. Linkage the same in both sets	2. Linkage complete in one set
$c(=ABAB)$	$(r+1)^2(4c+i+j) + r^2g+h$	$(r+1)(4c+i+j) + rg$
$d(=ABAb)$	$(r+1)^2(4d+i+k) + r^2h+g$	$(r+1)(4d+i+k) + rh$
$e(=aBaB)$	$(r+1)^2(4e+j+l) + r^2h+g$	$(r+1)(4e+j+l) + rh$
$f(=abab)$	$(r+1)^2(4f+k+l) + r^2g+h$	$(r+1)(4f+k+l) + rg$
Total homozygotes	$2(r+1)^2(2c+2d+2e+2f+i+j+k+l) + 2(r^2+1)(g+h)$	$2(r+1)(2c+2d+2e+2f+i+j+k+l) + 2r(g+h)$
$g(=ABAb)$	$2(r^2g+h)$	$2rg$
$h(=ABaB)$	$2(r^2h+g)$	$2rh$
Total heterozygotes	$2(r^2+1)(g+h)$	$2r(g+h)$
$i(=ABAB)$	$2(r+1)^2i + 2r(g+h)$	$2(r+1)i + g+h$
$j(=ABaB)$	$2(r+1)^2j + 2r(g+h)$	$2(r+1)j + g+h$
$k(=abAb)$	$2(r+1)^2k + 2r(g+h)$	$2(r+1)k + g+h$
$l(=abaB)$	$2(r+1)^2l + 2r(g+h)$	$2(r+1)l + g+h$
Total mixed	$2(r+1)^2(i+j+k+l) + 8r(g+h)$	$2(r+1)(i+j+k+l) + 4(g+h)$
Total	$4(r+1)^2(c+d+e+f+g+h+i+j+k+l)$	$4(r+1)(c+d+e+f+g+h+i+j+k+l)$

Table 31. Self-fertilization. Formulae for the zygotic constitution of the population derived from original parents *ABab* by any number n of successive self-fertilizations.

Let r = the linkage ratio

n = the number of successive self-fertilizations.

$$u = \frac{r}{2(r+1)}$$

$$v = \frac{r^2+1}{2(r+1)^2}$$

$$w = \frac{r^2-1}{2(r+1)^2}$$

The proportions of the 10 diverse classes of zygotes are designated by the letters c to l , as in table 1. Then after n successive generations of self-fertilization:

	Column 1. Linkage = r in both sets of gametes	Column 2. Linkage complete in one of the sets of gametes
Total homozygotes	$\frac{2^{n+1}-1}{2^{n-1}} + v^n$	$\frac{2^{n+1}-1}{2^{n-1}} + u^n$
$c(=ABAB)$	$\frac{2^{n+1}-1}{2^{n-1}} + \frac{v^n + w^n + w^{n-1} + w^{n-2} + \dots + w}{4}$	$\frac{2^{n+1}-1}{2^{n-1}} + \frac{u^n + u^{n-1} + u^{n-2} + \dots + u}{4}$
$d(=AbAb)$	$\frac{2^{n+1}-1}{2^{n-1}} + \frac{v^n - w^n - w^{n-1} - w^{n-2} - \dots - w}{4}$	$\frac{2^{n+1}-1}{2^{n-1}} + \frac{u^n - u^{n-1} - u^{n-2} - \dots - u}{4}$
$e(=aBaB)$	$= d$	$= d$
$f(=abab)$	$= c$	$= c$
Total heterozygotes	v^n	u^n
$g(=ABab)$	$\frac{v^n + w^n}{2}$	u^n
$h(=AbaB)$	$\frac{v^n - w^n}{2}$	0
Total mixed	$\frac{1}{2^{n-1}} - 2v^n$	$\frac{1}{2^{n-1}} - 2u^n$
$i(=ABAb)$	$\frac{1}{2^{n+1}} - \frac{v^n}{2}$	$\frac{1}{2^{n+1}} - \frac{u^n}{2}$
$j = k = l = i$	$\frac{2^{n+1}}{2} - 2$	$\frac{2^{n+1}}{2} - 2$

If the original parents are *AbaB*:

The values for c and d are to be interchanged.

“ “ “ e “ “ “ “
 “ “ “ g “ h “ “ “ “

The values for the mixed (i , j , k , l) remain unchanged, also the values for total homozygotes; total heterozygotes; and total mixed.

SOME INTER- AND BACK-CROSSES OF F₁ OENOTHERA HYBRIDS¹

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¹ Genetical studies on *Oenothera*—VIII.

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In a former paper (DAVIS 1914), I presented data on a number of F_1 hybrids between species crosses of *Oenothera* chiefly with reference to the studies of Professor DE VRIES on the remarkable crosses between *Oe. biennis* and *Oe. muricata*, where for certain vegetative characters patroclinous tendencies are strongly exhibited. DE VRIES expressed the results in the F_1 generations, for the characters concerned, by the formulae $m \times b = b$ and $b \times m = m$.

It will be remembered that DE VRIES (1911, 1913) has given his conclusions respecting the inheritance of habit and foliage in the inter- and back-crosses by a number of formulae which for *biennis* and *muricata* read as follows:

		Simplified
Double reciprocal	$(b \times m) \times (m \times b) = b$	$m \times b = b$
“ “	$(m \times b) \times (b \times m) = m$	$b \times m = m$
Sesquireciprocal	$b \times (m \times b) = b$	$b \times b = b$
“	$(b \times m) \times b = b$	$m \times b = b$
“	$m \times (b \times m) = m$	$m \times m = m$
“	$(m \times b) \times m = m$	$b \times m = m$
Iterative	$b \times (b \times m) = m$	$b \times m = m$
“	$(b \times m) \times m = m$	$m \times m = m$
“	$m \times (m \times b) = b$	$m \times b = b$
“	$(m \times b) \times b = b$	$b \times b = b$

By reducing the expressions which stand for the F_1 hybrids in accordance with the statement that $m \times b = b$ and $b \times m = m$ there is obtained the simplified formulae placed in the second column. The striking feature of the situation is the conclusion of DE VRIES that the pollen involved in all of these combinations makes the same impression whether it is from the species or from an F_1 hybrid and the impression is always in large measure a patroclinous dominance as to features of habit and foliage.

The dominance of the pollen parent expressed in the F_1 hybrids while at times conspicuous is, nevertheless, not an absolute dominance, but is relative in degree, as was shown by the analysis of the F_1 hybrids de-

scribed in my former paper (DAVIS 1914). I was unable to find evidence that a morphological character of either species in the crosses studied was ever passed on to the F_1 hybrids exactly as represented in either of the parents. When the resemblance to one of the parents has been strongest there has always been some trace of the influence of the other species. I was not convinced that the exact duplication of a parental character was ever attained in the F_1 hybrids of the material under consideration, which included crosses between *biennis* and *muricata*, *biennis* and *Franciscana*, *biennis* and *grandiflora*, and between *muricata* and *gigas*.

The present contribution will describe some inter- and back-crosses involving the F_1 generations of the species crosses listed above. Unfortunately the cultures were grown a year or two before the methods of experimental germination had been devised which make it possible to obtain complete germination of *Oenothera* seeds (DE VRIES 1915, DAVIS 1915). Consequently the results here presented can make no claim to complete information on the possibilities of the crosses involved. The percentages of germination from the earth-sown seeds were in certain cases strikingly small and I have since been able to establish from experimental germinations in Petri dishes the degrees of seed fertility that are inherently possible. This data is here included in comparison with the percentages of germination actually obtained from seed in the earth. Information on the facts of seed germination are essential to final conclusions in genetical work on hybrids where the amount of seed sterility is as great as in this material of *Oenothera*.

Especially necessary is this information on the crosses between *biennis* and *muricata* since these hybrids present an extraordinary amount of seed sterility together with much delayed germination. Consequently, earth-sown cultures of these hybrids frequently very imperfectly give the possibilities of the sowing as to numbers of individuals and we do not know how representative may have been the types obtained. Therefore, the results of my studies have no value as expressions of numbers and ratios and it is more than doubtful whether all of the types or classes represented by viable seeds actually materialized in the cultures. This criticism applies with equal force to the data presented by Professor DE VRIES. I have, however, no hesitation in giving my results, imperfect as they are, since I can at least indicate in certain measure the degree of imperfection, and the data as they stand have direct bearing on the studies of DE VRIES.

HYBRIDS INVOLVING *OENOTHERA BIENNIS* L. AND *OE. MURICATA* L.

- (a) Double reciprocal (*biennis* \times *muricata*) \times (*muricata* \times *biennis*),
cultures 14.43a and 14.43c

The seeds of this cross were obtained by pollinating 2 plants of culture 13.33 (F_1 , *biennis* \times *muricata*, DAVIS 1914, p. 176, figs. 11, 13, 15) from plants of culture 13.34 (F_1 , *muricata* \times *biennis*, DAVIS 1914, p. 176, figs. 10, 12, 14). The harvest was exceedingly small, as DE VRIES has also reported, very few seeds being developed and these only in the lower portions of the capsules. The seeds, however, were large and many were twice as long as broad. Plants 13.33a and 13.33c gave respectively 21 seeds from 4 capsules and 52 seeds from 7 capsules.

The germination of the seeds sown in earth, pans kept for 9 weeks,

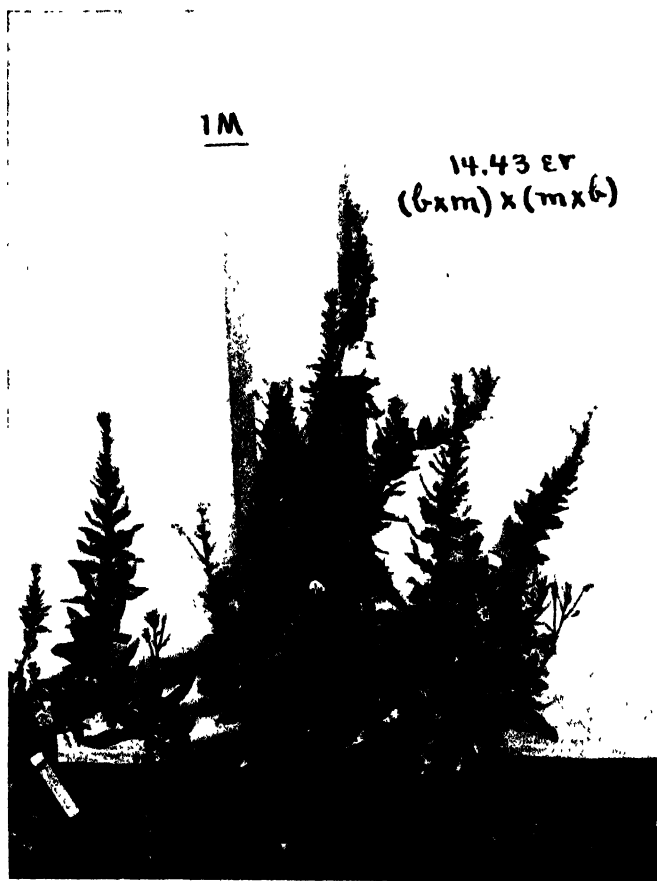


FIGURE 1.—Double reciprocal (*biennis* \times *muricata*) \times (*muricata* \times *biennis*). Type 2, *muricata*-like in habit, foliage, inflorescence, and buds. Self-sterile.

was extraordinarily poor. From the 21 seeds of plant 13.33a only 2 seedlings appeared, culture 14.43a, and the 52 seeds of plant 13.33c gave only 6 seedlings, culture 14.43c. The seedlings all reached maturity, a total of 8 plants from 73 seeds.

According to DE VRIES's formula, $(b \times m) \times (m \times b) = b$, all of the 8 plants should have been similar and *biennis*-like in habit and foliage, but, to my surprise, each of the two cultures presented two types sharply distinguished, which happened to be distributed in equal numbers (culture 14.43a 1 + 1, culture 14.43c 3 + 3). The points of contrast were not noted until maturity, since as rosettes the plants were similar and *biennis*-like. The striking differences between the two types are tabulated below and comparison may readily be made with a similarly arranged statement of the characters of *biennis* and *muricata* (DAVIS 1914, p. 174).

Double reciprocals (*biennis* \times *muricata*) \times (*muricata* \times *biennis*)

Type 1, *biennis*-like but less vigorous.

Mature plants. About 0.7 m high, similar to *biennis* in habit, but smaller, less vigorous and with fewer branches. Papillae on stem green as in *biennis*.

Foliage. Leaves resembling those of *biennis* in form and color but generally smaller.

Inflorescence. Bracts $\frac{1}{4}$ — $\frac{1}{2}$ length of mature buds, in form similar to *biennis* (fig. 3, 14.43cg). Younger buds projecting beyond the bracts as in *biennis*.

Mature buds. About 5 cm long, *biennis*-like in form, in the cone being scarcely angled, in the slender, spreading sepal tips, and in pubescence. (See Fig. 3, 14.43cg.)

Petals. 1.4 cm long, smaller than those of *biennis* (2—2.3 cm).

Type 2, in important respects *muricata*-like.

Mature plants. About 1.2 m high, habit of *muricata* but more branched and stocky, exceptional vegetative vigor (fig. 1). Papillae on stem red as in *muricata*.

Foliage. Leaves toothed and keeled as in *muricata* but broader (figs. 1 and 2), color a somewhat darker green.

Inflorescence. Bracts $\frac{2}{3}$ — $\frac{3}{4}$ length of mature buds, in form similar to *muricata* (fig. 3, 14.43cr). Bracts projecting beyond the younger buds (fig. 2) as in *muricata*.

Mature buds. About 6 cm long, larger than *muricata* but similar in form, in stout cone strongly 4-angled, and in thick appressed sepal tips. (See fig. 3, 14.43er.) Pubescence very heavy.

Petals. 1.4 cm long, somewhat larger than those of *muricata* (1—1.3 cm).

- | | |
|--|---|
| Stigma lobes. 5 mm long, about 3 mm below tips of anthers, similar to <i>biennis</i> . | Stigma lobes. 7 mm long, about 3 mm below tips of anthers, much longer and lower than in <i>muricata</i> . |
| Ovaries. Papillae green. | Ovaries. Papillae red. |
| Capsules. 2.3—2.5 cm long, similar to those of <i>biennis</i> . Self fertile, giving a large yield of seeds. | Capsules. Self sterile, 40 operations to self-pollinate all failures, occasional small capsules developed from open pollinations. |
| Pollen. 3-lobed and about 50% shriveled as in <i>biennis</i> . | Pollen. Perhaps 90% shriveled, the various-sized grains mostly 4-6 lobed. |

In view of the conclusions of DE VRIES it is very interesting that my cultures of this double reciprocal should have given two types so distinct as those just described. DE VRIES (1913, pp. 89, 90) reports on a culture of 25 plants all similar and *biennis*-like as in my type 1; he did not obtain type 2 with its resemblance in many points of morphology to *muricata*. It may therefore be questioned whether DE VRIES is correct



FIGURE 2.—Inflorescence of double reciprocal, type 2, (*biennis* × *muricata*) × (*muricata* × *biennis*), shown in fig. 1, *muricata*-like in foliage, bracts and buds.

in concluding for this double reciprocal that the characters of the *muricata* species are wholly set aside.

As previously stated, from the total of 73 seed-like structures sown in the earth only 8 seedlings appeared after 9 weeks, a germination of 11 percent. I had no seeds remaining to test experimentally the ratio of viable seeds when germination is forced to completion, but judging from my results in other crosses involving *biennis* and *muricata* the percentage of viable seeds should be much greater. It will become a matter of interest, when this cross is repeated and the seeds forced to complete germination, to see whether other types besides the two here reported may be found and a greater degree of segregation established. Since there is in the parent reciprocals, $b \times m$ and $m \times b$, a marked loss of vigor over the parents, *biennis* and *muricata*, and an unusually high degree of pollen sterility, and in the double reciprocal an exceptionally low yield of seeds there would seem to be the probability that large numbers of zygotic combinations are eliminated through the extraordinary mor-

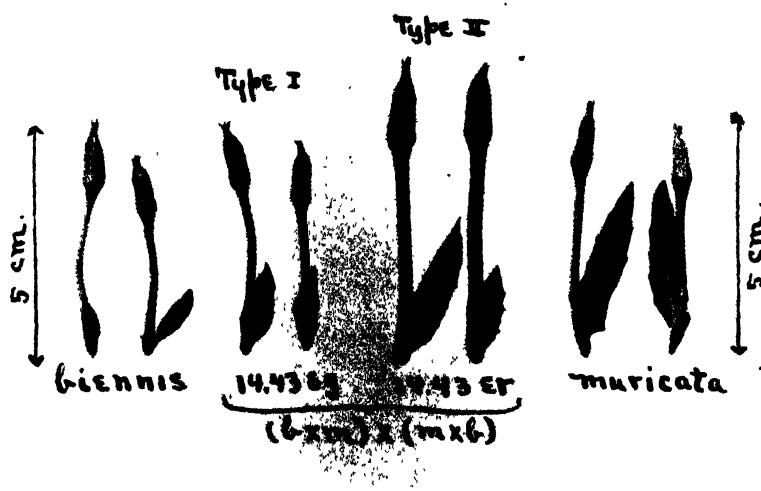


FIGURE 3.—Comparison of the buds and bracts of the two types of double reciprocals (*biennis* \times *muricata*) \times (*muricata* \times *biennis*). Type I similar to *biennis*. Type 2 resembling *muricata*.

talities of gametes and zygotes. It is along these lines that the peculiarities of this double reciprocal seem to me more likely to be understood rather than by the hypothesis put forward by DE VRIES.

I selfed a plant of type I (14.4363), the *biennis*-like segregate, and the following year obtained 38 seedlings from 304 seeds sown in the

earth, pans kept for 9 weeks, a germination of 12 percent. A subsequent experimental test in Petri dish of 477 seeds from the same harvest showed that 89 percent were actually viable. The 38 seedlings gave a culture, 15.43g, of 36 plants, 35 of which were *biennis*-like as DE VRIES described while 1 developed into a narrow-leaved weak type which failed to flower.

The 4 plants representative of type 2 were very interesting on account of their great vegetative vigor as well as for the numerous characters suggestive of *muricata*, and their complete self-sterility was surprising. The facts of this vigor together with the great amount of shriveled pollen (about 90 percent), most of which consisted of 4—6-lobed grains instead of the usual 3-lobed form suggest that the plants had some unusual chromosome complex which failed to behave properly at the time of reduction, after the manner characteristic of triploid forms of *Oenothera*.

(b) Double reciprocal, (*muricata* \times *biennis*) \times (*biennis* \times *muricata*)

I have twice been prevented from making this cross by the fact that in my garden the plants of the reciprocal *biennis* \times *muricata* produced pollen for so short a time that they became completely sterile before the cultures of *muricata* \times *biennis* had come to flower and were ready for a cross-pollination. In 1913 the reciprocal *biennis* \times *muricata* was represented by 92 plants (culture 13.33), as described in my earlier paper (DAVIS 1914, pp. 176-188). The culture came to flower towards the last of June, producing then less than $\frac{1}{2}$ as much pollen as might be expected from the size of the anthers. By the middle of July pollen was no longer shed, the anthers drying up to small shriveled structures.

Hoping to increase the output of pollen and to lengthen the time of its production I grew in 1914 the same reciprocal, dividing the plants into three groups and heavily treating each with a different type of fertilizer sold by Baugh and Sons Company. The fertilizers used, about 1 kilogram to the square meter, were (1) Baugh's raw bone meal, phosphoric acid 21.5%, ammonia 4.5%, (2) Baugh's balanced plant food, phosphoric acid 10.5%, ammonia 2%, potash 7%, (3) Baugh's high grade potato grower, phosphoric acid 8%, ammonia 4%, potash 10%. Although I obtained somewhat larger plants by this treatment there was apparently no improvement in the amount of pollen formed.

The reverse reciprocal, *muricata* \times *biennis*, also exhibited a similar but not quite so high a degree of pollen sterility and treatment with the same fertilizers in 1914 also failed to improve materially the output of pollen.

(c) Sesquiereciprocal, *biennis* \times (*muricata* \times *biennis*)

I was unable to make this cross successfully, taking the pollen from culture 14.34 (*muricata* \times *biennis*); 15 attempts during the middle of July gave no seed.

(d) Sesquiereciprocal, (*biennis* \times *muricata*) \times *biennis*, culture 15.31

Pollination of plants in culture 14.33 (*biennis* \times *muricata*) from *biennis* resulted in a fair harvest. Sowings in earth of 267 seeds from 7 capsules gave after 9 weeks a culture consisting of 25 seedlings, a germination of 9 percent. A record of complete germination in Petri dish presented 132 seedlings from a sowing of 282 seed-like structures,

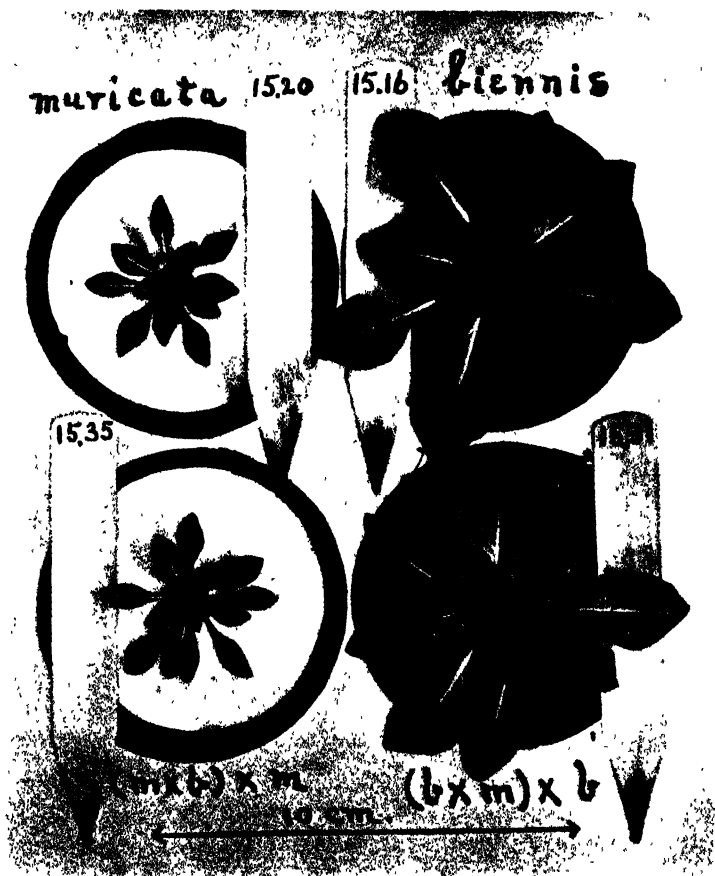


FIGURE 4.—A contrast of sesquiereciprocal (*biennis* \times *muricata*) \times *biennis*, culture 15.31, and (*muricata* \times *biennis*) \times *muricata*, culture 15.35, the former similar to *biennis* (15.16 above), the latter similar to *muricata* (15.20 above).

germination 46 percent. The 25 seedlings grew into mature plants uniform throughout all stages of development and at all times *biennis*-like although with apparently a somewhat greater vigor. A comparison in fig. 4 of the rosette 15.16 with 15.31 will show how close is the resemblance of the hybrid to *biennis*. These observations are in accord with the results of DE VRIES, but since the germination in the earth was so poor the cross should be repeated and cultures grown from seed forced experimentally to a complete expression of seed viability.

(e) Sesquireciprocal, *muricata* \times (*biennis* \times *muricata*)

The fact that pollen formation in the F_1 hybrid, *biennis* \times *muricata* (culture 14.33), ceased after the middle of July, made it impossible to accomplish this cross, since *muricata* in my garden comes to flower later in the summer.

(f) Sesquireciprocal, (*muricata* \times *biennis*) \times *muricata*, culture 15.35

There were sown in the earth 246 seeds from 5 capsules, which after 9 weeks gave 43 seedlings (culture 15.35), a germination of 17 percent. An experimental test of seed germination forced to completion resulted after 7 weeks in 198 seedlings from about 498 seed-like structures, germination about 40 percent. After the 43 green plants had been potted there began to appear in these pots seedlings with white cotyledons which promptly died; 23 of these were recorded before the green plants were set out in the garden. Since it is my habit to pot cultures in soil seed-sterile, and since these etiolated seedlings or other forms appeared in none of my other cultures I am forced to conclude that they represented a class derived from seeds carried over during the potting of the green plants and therefore the result of delayed germination. Such classes of etiolated seedlings are in my experience not uncommon from hybrids of *Oenothera*.

Of the green plants, 42 came to maturity and were in all points of morphology similar to *muricata*, but more vigorous, larger-leaved, and more fertile, producing capsules in abundance. The resemblance of the young rosettes to those of *muricata* is shown in fig. 4 (compare 15.35 with 15.20). Thus my observations on the green plants from incomplete germination conforms entirely to DE VRIES's conclusion that $(m \times b) \times m = m$, but I believe that a culture grown from seed experimentally forced to a complete germination would show at least a class of etiolated seedlings with the possibilities of other types.

(g) Iterative, *biennis* \times (*biennis* \times *muricata*), culture 15.32

The small amount of pollen produced by the F_1 , *biennis* \times *muricata*, made it difficult to obtain seed of this cross; 12 attempts at pollination gave 2 capsules with a total of 22 seeds. From the 22 seeds sown in earth only 1 seedling appeared after 9 weeks, a germination of 4.5 percent. The single seedling developed into a fine plant *muricata*-like in all points of morphology, but larger-leaved, more vigorous and highly fertile in its seed production. DE VRIES (1913, p. 95) obtained with very much larger cultures plants similar to the F_1 *biennis* \times *muricata* but he gives no data on the seed fertility following the cross $b \times (b \times m)$. My difficulty in obtaining seed together with the low germination in earth leads me to believe, either that all of the classes of viable seeds have not yet been germinated, or that lethal factors eliminate classes of gametes and zygotes.

(h) Iterative, (*biennis* \times *muricata*) \times *muricata*, culture 15.33

From 212 seeds, contents of 6 capsules, sown in the earth, I obtained after 9 weeks only 2 seedlings, a germination of 0.9 percent. A test in a Petri dish of 292 seeds from the same harvest gave after 7 weeks a complete germination of 42 seeds or 14 percent. One of the seedlings developed into a vigorous, highly fertile plant, *muricata*-like in morphology but larger-leaved; the other plant was dwarfed and weak, failing to flower, but with foliage similar to *muricata*. DE VRIES (1913, p. 96), who was fortunate in having very much larger cultures, reports that the plants without exception were of the type of the F_1 , *biennis* \times *muricata*. The obvious habit of delayed germination will make necessary further studies of this cross from seeds forced to complete germination, and the low percentage of viable seeds emphasizes the problems of gametic and zygotic sterility which run through so much of the work on *Oenothera* genetics.

(i) Iterative, *muricata* \times (*muricata* \times *biennis*), culture 15.36

A sowing of 198 seeds from 6 capsules gave after 9 weeks in earth 51 seedlings, germination 25.7 percent. By the time the rosettes were $\frac{1}{4}$ grown it was evident that their characters were intermediate between those of the parents (in fig. 5 compare 15.36 with 15.16 and 15.20), and similar to the rosettes of the F_1 hybrid *muricata* \times *biennis* (see DAVIS 1914, fig. 2, *muricata* \times *biennis*). The 51 seedlings produced mature plants uniform in appearance and also similar to the F_1 *muricata* \times *biennis*.

It will be remembered from my earlier paper (DAVIS 1914, pp. 176-181, figs. 10, 12, 14, 15) that this hybrid, *muricata* \times *biennis*, was patroclinous only in so far that the foliage of the rosettes and mature plants resembled more strongly that of the pollen parent, but that this resemblance was very far from a duplication of the characters of *biennis* since the leaves were intermediate in form and size. This hybrid was markedly matroclinous in the length of the bracts relative to the length of the buds and in the form of the sepal tips. Now the iterative hybrids presented these same characters to so similar a degree that the formula $m \times (m \times b) = (m \times b)$ expresses very accurately the facts, and like the cross $m \times b$ the iteratives were highly sterile. My results are apparently in full accord with those of DE VRIES but I should emphasize the fact that none of the characters of either parent were represented in pure form in the hybrids. The relatively low seed fertility and exceedingly high degree of pollen sterility strongly suggest that the hybrids may be representative of the only class able to survive in fair numbers the conditions of high mortality among the gametes and zygotes.

(j) Iterative, (*muricata* \times *biennis*) \times *biennis*, culture 15.34

These hybrids were of exceptional interest since they presented the same characters as the iterative *muricata* \times (*muricata* \times *biennis*) just described. From 217 seeds sown in earth, contents of 4 capsules, 47 seedlings were obtained after 9 weeks, a germination of 21.6 percent. From the fact that a sowing of about 373 seeds in a Petri dish gave after 4 weeks 73 seedlings, a germination of 19.5 percent, it would seem as though the germination in the earth must have been essentially complete. The $\frac{1}{4}$ -grown rosettes were intermediate between the parents (in fig. 5 compare 15.34 with 15.16 and 15.20), indistinguishable from the rosettes of the iterative $m \times (m \times b)$ (in fig. 5, compare 15.34 with 15.36), and also similar to the F_1 hybrid $m \times b$ (see DAVIS 1914, fig. 2, *muricata* \times *biennis*). All of the 47 seedlings developed into mature plants, uniform and of the same type as the iterative $m \times (m \times b)$ and the F_1 $m \times b$; they were likewise highly sterile. Thus my results with this iterative cross were the same as those of DE VRIES, but again the low seed fertility and high pollen sterility present factors that cannot be disregarded in an interpretation of the conclusions and lead me to believe that the plants so far grown are representative of only one class of hybrids, and that through the sterile and abortive seeds and by the pollen degeneration are eliminated other types of which we have no information.

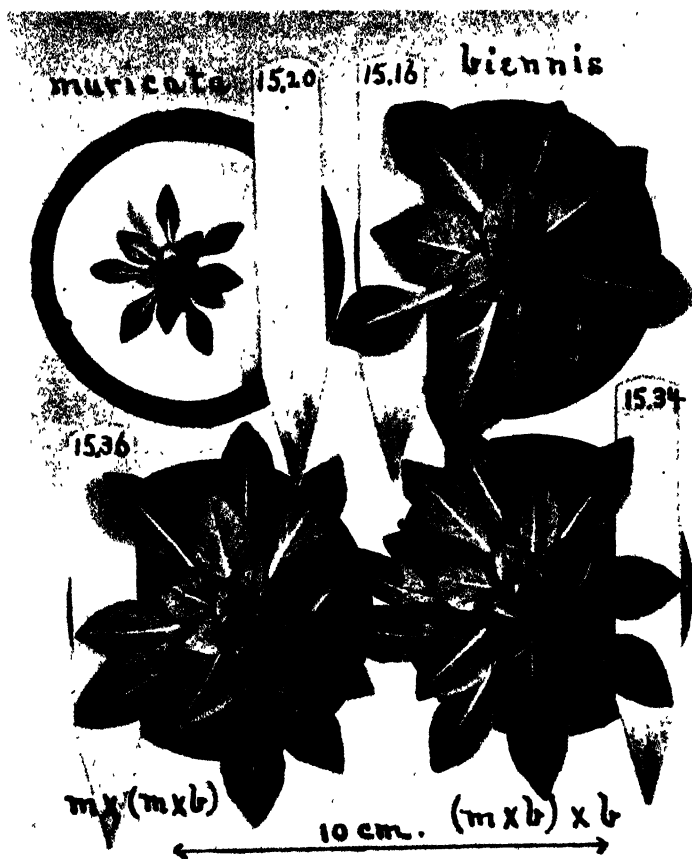


FIGURE 5.—Comparison of the iteratives *muricata* \times (*muricata* \times *biennis*), culture 15.36, and (*muricata* \times *biennis*) \times *biennis*, culture 15.34. These iteratives are essentially indistinguishable from one another and similar to the F_1 hybrid *muricata* \times *biennis*. They present rosette characters intermediate between those of the parents, *biennis* (15.16) and *muricata* (15.20) shown above.

(k) Remarks

I do not wish at this time to discuss the interesting theory of DE VRIES for the reported behavior of *biennis* and *muricata* in the inter- and back-crosses and also in the F_2 generations, since I am confident that we have not as yet the full data before us. My success in obtaining 2 types of plants from the double reciprocal ($b \times m$) \times ($m \times b$) where DE VRIES found only 1 and in finding a class of etiolated seedlings in the sesquiereciprocal ($m \times b$) \times m leads me to believe that cultures grown from seed forced to complete germination may show a greater variety

of forms. I also obtained in the iteratives $b \times (b \times m)$ and $(b \times m) \times m$ plants with the morphology of the *muricata* parent but even more vigorous and highly fertile while DE VRIES reports plants of the type of the F_1 , *biennis* \times *muricata*. The extent of delayed germination among these hybrids is undoubtedly very great and only by methods of experimental germination which preserve the residue of sterile structures for examination can we be certain that cultures exhibit the full possibilities of viable seeds. In table I there is given the data on seed germination in my cultures of hybrids involving *biennis* and *muricata* and a glance will show how low was the percentage of germination obtained from sowings in earth even though the seed pans were for the most part kept as long as 9 weeks. Of especial interest are the comparisons that may be made of 5 records of earth-sown cultures with experimental germinations from the same harvests in Petri dishes; 15.43g with *15.43g, 15.31 with *15.31, 15.35 with *15.35, 15.33 with *15.33, and 15.34 with *15.34. These records show generally that the sowings in earth brought forth only a small fraction of the viable seed.

TABLE I

Seed germination in crosses involving *Oenothera biennis* and *Oe. muricata*

Culture	Cross	Seeds sown	Sown in	Seedlings	Percent of germination	Duration of experiment
14.43	Double reciprocal, $(b \times m) \times (m \times b)$	73	Earth	8	11.0	9 weeks
15.43g	F_2 , Double reciprocal, 14.43eg selfed	403	Earth	38	12.0	9 weeks
*15.43g	F_2 , Double reciprocal, 14.43eg selfed	477	Petri dish	427	89.0	6 weeks
15.31	Sesquiereciprocal, $(b \times m) \times b$	267	Earth	25	9.0	9 weeks
*15.31	Sesquiereciprocal, $(b \times m) \times b$	282	Petri dish	132	46.0	6 weeks
15.35	Sesquiereciprocal, $(m \times b) \times m$	246	Earth	43	17.0	9 weeks
*15.35	Sesquiereciprocal, $(m \times b) \times m$	498	Petri dish	198	40.0	7 weeks
15.32	Iterative, $b \times (b \times m)$	22	Earth	1	4.5	9 weeks
15.33	Iterative, $(b \times m) \times m$	212	Earth	2	0.9	9 weeks
*15.33	Iterative, $(b \times m) \times m$	292	Petri dish	42	14.0	7 weeks
15.36	Iterative, $m \times (m \times b)$	198	Earth	51	25.7	9 weeks
15.34	Iterative, $(m \times b) \times b$	217	Earth	47	21.6	9 weeks
*15.34	Iterative, $(m \times b) \times b$	373	Petri dish	73	19.5	4 weeks
14.41	F_2 , <i>biennis</i> \times <i>muricata</i>	466	Earth	8	1.7	9 weeks
14.42	F_2 , <i>muricata</i> \times <i>biennis</i>	205	Earth	35	12.0	9 weeks
13.33	F_1 , <i>biennis</i> \times <i>muricata</i>	673	Earth	139	20.0	6 weeks
13.34	F_1 , <i>muricata</i> \times <i>biennis</i>	153	Earth	97	63.0	7 weeks

Delayed germination is, however, only one of the factors in the genetical problems of fertility presented by these interesting crosses. There was an immense amount of seed sterility presented in the records *15.31, *15.35, *15.33, and *15.34, as proved by the residue of seeds empty of contents and by numerous abortive structures of smaller size. Also, there is the wide-spread pollen degeneration which gives to these hybrids usually a remarkably small output of pollen, and possibly correlated with this is the large amount of ovule powder representing ovules which either were not fertilized or if fertilized failed to develop further. Until this data on gametic and zygotic sterility is assembled and understood in its cytological and physiological bearings we are in no position to hold more than tentative hypotheses. I am inclined to believe that the relatively few types so far described among these hybrids represent a limited number of classes able to survive the very extensive mortality among the gametes and zygotes. The number of classes is, I think, likely to be materially increased through cultures grown from seed forced experimentally to complete germination.

The interesting facts so far before us show that many of the characters of *biennis* and *muricata* are inherited in close correlation or, in other words, are closely linked, and this principle seems generally to be established by studies on *Oenothera* genetics. With respect to the crosses under consideration the combined results of DE VRIES and myself may be summarized as follows:

		DE VRIES	DAVIS
Double reciprocal	$(b \times m) \times (m \times b) =$	<i>biennis</i>	<i>biennis</i> (4 plants), and a sterile form somewhat <i>muricata</i> -like (4 plants)
Double reciprocal	$(m \times b) \times (b \times m) =$	<i>muricata</i>	No data
Sesquirectiprocal	$b \times (m \times b) =$	<i>biennis</i>	No data
Sesquirectiprocal	$(b \times m) \times b =$	<i>biennis</i>	<i>biennis</i> (25 plants)
Sesquirectiprocal	$m \times (b \times m) =$	<i>muricata</i>	No data
Sesquirectiprocal	$(m \times b) \times m =$	<i>muricata</i>	<i>muricata</i> (43 plants), and a class of etiolated seedlings (23 plants)
Iterative	$b \times (b \times m) =$	<i>biennis</i> \times <i>muricata</i>	<i>muricata</i> (1 plant)
Iterative	$(b \times m) \times m =$	<i>biennis</i> \times <i>muricata</i>	<i>muricata</i> (2 plants)
Iterative	$m \times (m \times b) =$	<i>muricata</i> \times <i>biennis</i>	<i>muricata</i> \times <i>biennis</i> (51 plants)
Iterative	$(m \times b) \times b =$	<i>muricata</i> \times <i>biennis</i>	<i>muricata</i> \times <i>biennis</i> (47 plants)

The points of difference in the conclusions as tabulated above indicate to me that further studies are likely to increase the number of types

which will be obtained from these crosses when cultures have been grown in which we may feel certain that all of the seeds have germinated. The results so far indicate that the characters of the hybrids for the most part, as represented in the viable seeds, are similar to one or the other of the parents or similar to the F_1 hybrids. If the characters should prove to be correlated with little variation from so simple an arrangement the different types of viable gametes formed would be relatively few in number, and the data on sterility both gametic and zygotic may give, when assembled, the key to the peculiarities of these interesting hybrids.

HYBRIDS INVOLVING *OENOTHERA BIENNIS* L. AND *OE. FRANCISCANA* BARTLETT

My studies on hybrids between *Oenothera biennis* and *Oe. Franciscana* have had for me the greatest interest with respect to the evidence for the segregation of parental characters shown in the F_2 generation (DAVIS 1916), and with reference to the *Lamarckiana*-like forms that may be found among these segregates. I have, however, grown a full set of double reciprocals, sesquireciprocals and iterative hybrids from crosses with the race *Franciscana* E. The characters of *Franciscana* will be found contrasted with those of *biennis* in the paper on the F_2 generations of that cross (DAVIS 1916, pp. 206, 207), and the characters of the F_1 reciprocal hybrids are compared in the earlier paper (DAVIS 1914, pp. 190, 191). I shall now only report briefly the chief features of the back- and inter-crosses, following the order of descriptions as just given in the account of the same crosses between *biennis* and *muricata*. It will be noted that the results do not follow consistently the formulae given by DE VRIES for the inter- and back-crosses of the F_1 reciprocals of *biennis* and *muricata*; compare p. 156 with p. 175.

- (a) Double reciprocal, (*biennis* \times *Franciscana* E) \times (*Franciscana* E \times *biennis*), culture 15.62

A sowing of 302 seeds, contents of 2 capsules, in earth, gave after 9 weeks 72 seedlings, germination 23.8 percent. A test of seed viability in a Petri dish produced 342 seedlings from about 657 seed-like structures with an additional residue of 130 abortive seeds, germination 52 percent. Shoots were developed from 51 rosettes, 11 of which were *biennis*-like, the others mostly resembling *Franciscana* or having characters intermediate between the parents; there was an eventual mortality of 21 plants mostly from a group of dwarfs. The stems all had the red papillae of *Franciscana*. The foliage on shoots from the *biennis*-

like rosettes was similar to *biennis* and the buds, flowers and capsules were also like those of *biennis*. The *Franciscana*-like rosettes produced plants with foliage and buds of this parent but fully half of the plants had flowers of the size and form of *biennis*. The culture thus, failing to hold to one type, clearly differentiated several classes of hybrids. The low germination of the earth-sown culture does not justify further discussion.

(b) Double reciprocal, (*Franciscana* E \times *biennis*) \times (*biennis* \times *Franciscana* E), culture 15.61

The seed germination of this cross in the earth was 30 percent, and that of an experimental test 34 percent, so there is some reason for regarding the culture as fairly representative. There appeared at the end of 8½ weeks 73 seedlings from a sowing of 243 seeds, contents of 2 capsules. Of the 63 rosettes which survived 3 were *biennis*-like, 15 intermediate, 38 *Franciscana*-like and the others were narrow-leaved dwarfish types. Shoots were sent up from 63 rosettes and all were red papillate as in *Franciscana*. One of the *biennis*-like rosettes produced a plant with foliage, buds and capsules of this parent but with a petal size and stigma relation of *Franciscana*; the other two rosettes developed into plants which resembled *Franciscana* in foliage, buds and capsules but had the smaller petals and shorter style of *biennis*. The *Franciscana*-like rosettes and those intermediate all developed shoots similar to *Franciscana* in foliage and buds but with flower size and structure *biennis*-like in 33 of the 53 plants. The culture at maturity with the exception of 1 plant consisted then of types *Franciscana*-like as to foliage, bud form and capsules, but with a wide range of flowers from a size and structure as in *biennis* to flowers indistinguishable from those of *Franciscana*. The segregation was remarkably clear-cut in 17 plants which were very close to the *Franciscana* parent, but as a whole the culture was far from uniform.

(c) Sesquiereciprocal, *biennis* \times (*Franciscana* E \times *biennis*), culture 15.64

This cross proved to be of exceptional interest for its well defined segregates and especially for the appearance of green-stemmed plants in contrast to those with red papillae. A sowing in earth of 151 large seeds from 1 capsule produced after 8½ weeks 27 seedlings, a germination of about 18 percent. Experimental germination of 432 seeds gave 323 seedlings, about 75 percent, so that the earth-sown culture was

very far from representative of the seed viability. Of the rosettes, 11 were *biennis*-like, 11 intermediate, 1 *Franciscana*-like and 4 were narrow-leaved dwarfs. The shoots from the *biennis*-like rosettes were green (papillae not red) and all of these plants were also *biennis*-like in foliage, buds, flowers and capsules; they constituted a remarkable class of segregates in all respects similar to the *biennis* parent. The rosettes intermediate in character or *Franciscana*-like developed shoots with red papillae and likewise presented foliage and buds as in *Franciscana*, but all had the smaller petals and shorter styles of *biennis*. Thus about $\frac{1}{2}$ of the plants were like the *biennis* parent, while *Franciscana* characters of stem coloration, foliage and buds, appeared in the remainder of the culture.

(d) Sesquireciprocal, (*biennis* × *Franciscana* E) × *biennis*, culture 15.67

This cross gave a progeny remarkably uniform and possibly fairly representative of the viable seeds. The earth-sown culture consisting of 159 seeds from 1 capsule gave after 12 weeks 46 seedlings, germination about 29 percent; in a Petri dish 593 seeds produced 193 seedlings, germination 32.5 percent. As rosettes 44 of the plants were *biennis*-like and 2 were narrow-leaved dwarfs which died; 40 plants of the *biennis*-like group came to maturity. They were strong plants similar to *biennis* in habit, foliage, bud and flower structure, but with longer capsules (2.5-3 cm) and all with the red papillae of *Franciscana*. Thus the color peculiarity of *biennis* (green stems) together with the short capsules failed to segregate with the other conspicuous characters of this parent species.

(e) Sesquireciprocal, *Franciscana* E × (*biennis* × *Franciscana* E),
culture 15.70

This cross was represented by a relatively large number of plants; 248 seeds, from 1 capsule, gave in the earth after $8\frac{1}{2}$ weeks 124 seedlings, germination 50 percent. A test in Petri dish of 603 seed-like structures resulted in 533 seedlings, germination 88 percent. The culture matured 90 plants and was uniformly *Franciscana*-like in the form of the rosette, in having red papillae over the stems in the form of the foliage, bud tips and capsules. There was a wide range of flower size, most of the plants approaching *biennis* in having smaller petals and a lower position of the stigma, and there was likewise much variation in the size of the leaves; 15 plants were *Franciscana*-like in all respects. A group of 22 backward plants remained as dwarf rosettes.

- (f) Sesquiereciprocal, (*Franciscana* E \times *biennis*) \times *Franciscana* E, culture 15.65

From 154 large seeds, contents of 1 capsule, sown in the earth there were obtained after 8½ weeks 41 seedlings, a germination of 26 percent; tested in Petri dish 220 seeds gave 100 seedlings, germination 45 percent. The culture matured 37 plants of which 1 was green-stemmed and *biennis*-like in all other respects except for larger capsules and a weak branching. The other 36 plants were uniformly *Franciscana*-like as rosettes, in foliage, buds and in having red papillae. They exhibited, however, many flowers approaching *biennis* in size and position of stigma; 16 plants were in all respects *Franciscana*-like.

- (g) Iterative, *biennis* \times (*biennis* \times *Franciscana* E), culture 15.68

In this cross the germination of 108 seeds in earth, giving 40 seedlings, 37 percent, after 8½ weeks was higher than that of 145 seed-like structures in a Petri dish, 45 seedlings, 31 percent. A high mortality among the rosettes, however, reduced the number of plants that matured to 23. These were all *Franciscana*-like as rosettes, in foliage, buds, and capsules, and in having red papillae. The flower size was generally smaller than that of *Franciscana* and the leaves were frequently larger; 9 plants were quite indistinguishable from *Franciscana*. A single narrow-leaved dwarf was present.

- (h) Iterative, (*biennis* \times *Franciscana* E) \times *Franciscana* E, culture 15.69

This cross furnished another example of an earth-sown culture giving a germination equal to the test in a Petri dish. Sowings of 177 seeds after 8½ weeks resulted in 99 seedlings, germination 56 percent; about 300 seed-like structures in a Petri dish gave 171 seedlings, germination 57 percent. There matured 96 plants all *Franciscana*-like as rosettes, in foliage, in buds, and in having red papillae, but the flower size was generally smaller than that of *Franciscana* and the stigma frequently occupied a somewhat lower position; 11 plants were in all respects *Franciscana*-like. The cross then reproduced essentially the characters exhibited by the iterative *biennis* \times (*biennis* \times *Franciscana* E), and like the latter consisted of exceptionally vigorous plants frequently larger-leaved than the parent which it so closely resembled in its vegetative characters. Dwarfs were represented by 1 narrow-leaved plant.

- (i) Iterative, *Franciscana* E \times (*Franciscana* E \times *biennis*), culture 15.66
 . A sowing of 263 seeds from one capsule in earth gave after 8½

weeks 126 seedlings, germination 48 percent; experimentally tested, 741 seeds gave 581 seedlings, germination 78 percent. The presence of 6 etiolated rosettes which died, together with further mortality, reduced the number of plants that matured to 111; of these all agreed in having red papillae on the stems. In other respects the culture presented wide divergence of types; 17 plants had foliage, bud tips and capsules *biennis*-like, and of these, 3 plants bore flowers of the size and form of *biennis*, 7 were intermediate between the parents, and 7 had flowers similar to those of *Franciscana*; 94 plants were *Franciscana*-like in foliage, bud tips and capsules, but of these only 26 had flowers with the size and form of *Franciscana*, 63 presenting flowers intermediate in structure, 4 essentially duplicating the flower type of *biennis* and 1 plant presenting smaller petals (1.4 cm). Thus none of the segregates fully represented *biennis*, since all had red papillae, but 26 were of the *Franciscana* type.

(j) Iterative, (*Franciscana* E \times *biennis*) \times *biennis*, culture 15.63

This cross resembled *biennis* in all respects except that the stems all bore the red papillae of *Franciscana* and the capsules, uniformly longer, were similar to those of the latter parent. From 206 seeds, contents of 2 capsules, sown in earth 100 seedlings appeared after 8½ weeks, germination 48.5 percent; in a Petri dish 238 seeds gave 188 seedlings, germination 79 percent. Only 45 plants grew to maturity, there being 40 etiolated dwarf rosettes which died and other plants which either remained as rosettes or failed to survive the summer. Of the 45 rosettes which sent up shoots 34 were *biennis*-like and the remainder had larger and more crinkled leaves somewhat as in *Lamarckiana*. The culture at maturity was remarkably uniform and *biennis*-like in foliage, buds, flower size and structure, but as noted above showed the red papillae of *Franciscana* together with *Franciscana*-like capsules (2.7-3 cm long).

(k) Remarks

The surprising feature of the double reciprocals, sesquireciprocals and iterative hybrids involving *biennis* and *Franciscana* E is the much greater variety of segregation exhibited as contrasted with that known for similar hybrids in which *biennis* and *muricata* are concerned. It is impossible to express the facts in simple formulae, but the most striking features are presented below.

Double reciprocal	$(b \times f) \times (f \times b)$	Type I, <i>biennis</i> -like except for red papillae (11 plants). Type II, <i>Franciscana</i> -like in red papillae, foliage and buds, but various as to flower form and size (40 plants).
	$(f \times b) \times (b \times f)$	Type I, <i>biennis</i> -like except for red papillae and large flowers (1 plant). Type II, generally <i>Franciscana</i> -like in red papillae, foliage and buds, but various as to flower form and size (62 plants).
Sesquireciprocal	$b \times (f \times b)$	Type I, <i>biennis</i> -like in all respects (11 plants). Type II, <i>Franciscana</i> -like in red papillae, foliage and buds, but with flowers similar to <i>biennis</i> (12 plants).
	$(b \times f) \times b$	<i>Biennis</i> -like except for red papillae and longer capsules (40 plants).
	$f \times (b \times f)$	<i>Franciscana</i> -like except for wide variation in flower size and form, most of the plants in this respect approaching <i>biennis</i> (90 plants).
	$(f \times b) \times f$	Type I, <i>biennis</i> -like (1 plant). Type II, <i>Franciscana</i> -like in red papillae, foliage and buds, but various as to flower form and size (36 plants).
Iterative	$b \times (b \times f)$	<i>Franciscana</i> -like except that flowers were generally smaller (23 plants).
	$(b \times f) \times f$	<i>Franciscana</i> -like except that flowers were generally smaller (96 plants).
	$f \times (f \times b)$	Type I, <i>biennis</i> -like except for red papillae and flowers various in form and size (17 plants). Type II, <i>Franciscana</i> -like in red papillae, foliage, buds, and capsules, but various as to flower form and size (94 plants).
	$(f \times b) \times b$	<i>Biennis</i> -like except for red papillae and longer capsules (45 plants). A group of 40 etiolated dwarf rosettes died early.

Comparison of these data with those given for the same crosses between *biennis* and *muricata* (page 169) will show at a glance how much more involved are the facts and how impossible it is to bring the conclusions into line with the simple formulae which DE VRIES offers for the hybrids between *biennis* and *muricata*. Does this more extensive segregation depend upon fundamental differences between the parent types, *Franciscana* and *muricata*? I venture to believe that it probably does not but that the much greater seed sterility of the *biennis-muricata* crosses masks a similar degree of segregation which has not been expressed in the small cultures so far obtained and may never be expressed because

of the extraordinary mortality among the gametes and zygotes of these hybrids.

To bring out clearly the greater degree of fertility in the *biennis-Franciscana* crosses I have prepared a statement, table 2, of my data on seed germination arranged so that it may be readily compared with table 1 which gives my data for the same crosses between *biennis* and *muricata*. It will be easily seen that the germination percentages of the *biennis-Franciscana* crosses are in general very much higher than those for the hybrids involving *biennis* and *muricata*. Thus the double reciprocal $(b \times f) \times (f \times b)$ in earth gave a germination of 23.8 percent while that of $(b \times m) \times (m \times b)$ was 11 percent; the sesquiereciprocal $(b \times f) \times b$ 29 percent and $(b \times m) \times b$ 9 percent; the iteratives $b \times (b \times f)$ 37 percent and $b \times (b \times m)$ 4.5 percent; $(b \times f) \times f$ 56 percent and $(b \times m) \times m$ 0.9 percent; $f \times (f \times b)$ 48 percent and $m \times (m \times b)$ 25.7 percent; $(f \times b) \times b$ 48 percent and $(m \times b) \times b$ 21.6 percent.

The table also shows some of the striking gains in percentage when seeds are germinated in Petri dishes; compare 15.62 with *15.62, 15.63 with *15.63, 15.64 with *15.64, 15.65 with *15.65, 15.66 with *15.66 and 15.70 with *15.70. In certain cases the germination in the Petri dishes was not so large as the germination in the earth; compare 15.68 with *15.68, and 15.38 with *15.38. Of especial interest is the comparison of 15.37 with *15.37 and 15.38 with *15.38 for the pans containing the earth-sown seeds were in these cultures kept for 16 months and the last seedlings appeared as late as 13 and 11 months after the sowing while $8\frac{1}{2}$ and $3\frac{1}{2}$ weeks respectively brought a complete germination in the Petri dishes.

In the segregation displayed by the crosses between *biennis* and *Franciscana* the following close correlations of characters were quite as conspicuous as the correlations displayed in the *biennis-muricata* crosses. (1) Plants *biennis*-like in all respects were found in the sesquiereciprocals $b \times (f \times b)$ and $(f \times b) \times f$. (2) *Biennis*-like classes, except for red papillae, were present in both double reciprocals, in the sesquiereciprocal $(b \times f) \times b$, and in the iteratives $f \times (f \times b)$ and $(f \times b) \times b$. (3) Plants *Franciscana*-like in red papillae, foliage and buds, constituted the entire cultures of the sesquiereciprocal $f \times (b \times f)$, and of the iteratives $b \times (b \times f)$ and $(b \times f) \times f$, and appeared as classes in the double reciprocals, the sesquiereciprocals $b \times (f \times b)$ and $(f \times b) \times f$, and in the iteratives $f \times (f \times b)$ and $(f \times b) \times b$. In view of the imperfect germination in these earth-sown cultures I do not believe that the data give all

TABLE 2

Seed germination in crosses involving *Oenothera biennis* and *O. Franciscana*

Culture	Cross	Seeds sown	Sown in	Seedlings	Percent of germination	Duration of experiment
15.62	Double reciprocal $(b \times f) \times (f \times b)$	302	Earth	72	23.8	9 weeks
*15.62	Double reciprocal $(b \times f) \times (f \times b)$	657	Petri dish	342	52	10 weeks
15.61	Double reciprocal $(f \times b) \times (b \times f)$	243	Earth	73	30	8½ weeks
*15.61	Double reciprocal $(f \times b) \times (b \times f)$	109	Petri dish	39	34	8 weeks
15.64	Sesquiereciprocal $b \times (f \times b)$	151	Earth	27	17	8½ weeks
*15.64	Sesquiereciprocal $b \times (f \times b)$	432	Petri dish	323	75	7 weeks
15.67	Sesquiereciprocal $(b \times f) \times b$	159	Earth	46	29	8½ weeks
*15.67	Sesquiereciprocal $(b \times f) \times b$	593	Petri dish	193	32	7 weeks
15.70	Sesquiereciprocal $f \times (b \times f)$	248	Earth	124	50	8½ weeks
*15.70	Sesquiereciprocal $f \times (b \times f)$	603	Petri dish	533	88	4 weeks
15.65	Sesquiereciprocal $(f \times b) \times f$	154	Earth	41	26	8½ weeks
*15.65	Sesquiereciprocal $(f \times b) \times f$	220	Petri dish	100	45	10 weeks
15.68	Iterative $b \times (b \times f)$	108	Earth	40	37	8½ weeks
*15.68	Iterative $b \times (b \times f)$	145	Petri dish	45	31	10 weeks
15.60	Iterative $(b \times f) \times f$	177	Earth	59	56	8½ weeks
*15.60	Iterative $(b \times f) \times f$	300	Petri dish	171	57	10 weeks
15.66	Iterative $f \times (f \times b)$	263	Earth	126	48	8½ weeks
*15.66	Iterative $f \times (f \times b)$	741	Petri dish	581	78	10 weeks
15.63	Iterative $(f \times b) \times b$	206	Earth	100	48	8½ weeks
*15.63	Iterative $(f \times b) \times b$	238	Petri dish	188	79	8 weeks
15.37	F_2 , <i>Franciscana</i> E \times <i>biennis</i>	396	Earth	195	49	16 months
*15.37	F_2 , <i>Franciscana</i> E \times <i>biennis</i>	682	Petri dish	513	52	8 weeks
15.38	F_2 , <i>biennis</i> \times <i>Franciscana</i> E	367	Earth	250	68	16 months
*15.38	F_2 , <i>biennis</i> \times <i>Franciscana</i> E	562	Petri dish	322	57	3½ weeks
14.51	F_2 , <i>Franciscana</i> B \times <i>biennis</i>	819	Earth	402	49	11 weeks
15.51	F_2 , <i>Franciscana</i> B \times <i>biennis</i>	921	Petri dish	761	82.6	3½ weeks
15.52	F_2 , <i>biennis</i> \times <i>Franciscana</i> B	623	Petri dish	438	70	3½ weeks
15.46	F_1 , <i>Franciscana</i> E \times <i>biennis</i>	955	Petri dish	875	91.6	5 weeks
15.47	F_1 , <i>biennis</i> \times <i>Franciscana</i> E	510	Petri dish	430	84	9 weeks
13.35	F_1 , <i>Franciscana</i> B \times <i>biennis</i>	652	Earth	328	50	4-7 weeks
15.44	F_1 , <i>Franciscana</i> B \times <i>biennis</i>	636	Petri dish	606	95	5½ weeks
13.36	F_1 , <i>biennis</i> \times <i>Franciscana</i> B	381	Earth	167	43.8	6-7 weeks
15.45	F_1 , <i>biennis</i> \times <i>Franciscana</i> B	440	Petri dish	304	69	6 weeks

of the possibilities of the viable seeds, but, such as they are, the records show a remarkable degree of linkage between certain characters.

I have throughout emphasized the fact that the characters of the rosettes, foliage, bud tips, capsules, and stem coloration (papillae either red or green) generally segregate clearly towards one or the other of the parents. There is, however, considerable variation in the size of organs, a variation extremely difficult to classify and probably subject to much fluctuation. Flower structure presented itself in a wide range

of size and relationships of anthers to stigmas, giving much less frequently conditions resembling the parents. Plants with red papillae were much more numerous than green-stemmed plants which were found only in the sesquireciprocals $b \times (f \times b)$ and $(f \times b) \times f$ where these plants in other respects were *biennis*-like. The plants of other crosses, *biennis*-like in all other respects, had red papillae. It is curious that in the sesquireciprocal $b \times (f \times b)$ the green-stemmed plants (11) were almost equal in number to those with red papillae (12), but the germination was only 17 percent in the earth-sown cultures while the tests in the Petri dish showed 75 percent of viable seeds.

HYBRIDS INVOLVING *OENOTHERA BIENNIS* L. AND *OE. GRANDIFLORA* SOLANDER

I am able to report only on the double reciprocals of the crosses between *Oenothera biennis* and *Oc. grandiflora*, the parent reciprocals being plants of the cultures (12.48 and 12.49) described in my paper of 1914, pp. 192-196, where will also be found a description of the race *grandiflora* D. The F_1 reciprocal crosses resembled the pollen parent and were consequently patroclinous (1) in the morphology of the rosettes and in the relative promptness with which the rosettes sent up their central shoots, (2) in the height and branching habit of the mature plants, (3) in the form of the leaves, (4) in the morphology of the inflorescence, (5) in the position of the stigma relative to the anthers, (6) in the time of flowering, (7) in the length of the capsules. Nevertheless, here as in other reciprocal crosses I failed to find certain evidence that any character of the pollen parent appeared in the F_1 hybrids in absolutely unmodified form; a matroclinous tendency was exhibited in the form of the sepal tips.

There will also be given a brief description of cultures in the F_2 from the F_1 plants, 12.48a, *grandiflora* D \times *biennis*, and 12.49a, *biennis* \times *grandiflora* D, which were the parents of the double reciprocals. This account is of considerable interest when taken in relation to the low percentage of germination obtained.

(a) Double reciprocal, (*biennis* \times *grandiflora* D) \times (*grandiflora* D \times *biennis*), culture 13.44

From a sowing in earth of 221 seeds, contents of 1 capsule, there appeared after $7\frac{1}{2}$ weeks 98 seedlings, a germination of 44 percent. About $\frac{1}{2}$ of the seedlings presented cotyledons partly or wholly etiolated and from among these a group of 30 weak dwarfs developed with a very short abortive root system and a close cluster of narrow leaves,



FIGURE 6.—A dwarf type from the F_2 of *grandiflora* D \times *biennis*, culture 13.41, and represented also in the F_2 of *biennis* \times *grandiflora* D, culture 13.42, and in the two double reciprocals, cultures 13.43 and 13.44. Rosettes a close cluster of narrow leaves generally somewhat etiolated and not more than 1—2 cm long, a very short abortive root system.

generally somewhat etiolated and mostly not more than 1-2 cm long (fig. 6). Many of these dwarfs promptly died and none grew sufficiently large to plant in the garden. There were set out 68 plants which as rosettes presented a varied assortment some tending towards the *biennis* and some towards the *grandiflora* parent; about 15 of these were more or less etiolated but later outgrew this peculiarity. As the culture approached maturity 21 plants exhibited a foliage, habit, and bud tips similar to *biennis* but were much taller plants (1.3-1.5 m high). The remaining 47 plants had narrow leaves intermediate between the parents and none so narrow as those of *grandiflora* D. The flowers exhibited a wide range, some being as small as those of *biennis* and with a similar position of the stigma at or below the level of the anther tips, others being large and with the stigma well beyond the anther tips as in *grandiflora* D. No correlations were discovered between the flower size and other features of morphology. The culture, therefore, was very far from uniform and showed abundant evidence of segregation. Its composition could not be expressed by the formula $(b \times g) \times (g \times b) = b$ which would be the analogue of the formula $(b \times m) \times (m \times b) = b$ given by DE VRIES for the same type of double reciprocal involving *biennis* and *muricata*. In the latter cross the percentage of viable seeds is much lower, a fact which suggests that high seed sterility or delayed germination is responsible for the uniform results obtained by DE VRIES.

(b) Double reciprocal, (*grandiflora* D \times *biennis*) \times (*biennis* \times *grandiflora* D), culture 13.43

A sowing of 217 seeds in earth, from 1 capsule, gave after 7½ weeks 104 seedlings, a germination of 47.9 percent. A class of 33 dwarfs appeared with very short narrow leaves (fig. 6) exactly similar to those in the other double reciprocal (culture 13.44) described above; these likewise were too weak to set out in the garden. There were developed 71 vigorous rosettes fairly uniform and intermediate between the parents but resembling *grandiflora* more than *biennis* especially since they showed extensive anthocyan coloration. At maturity the culture contained 19 plants similar in general morphology to *biennis* but with the anthocyan coloration of *grandiflora*; the other 52 plants had narrower leaves, but not so narrow as those of *grandiflora*, and all showed red coloration in spots and patches sometimes covering the greater part of the leaves. As in the other double reciprocal the flowers varied widely but were mostly of the size of *biennis* and with a similar position of the stigma; a few plants had large flowers of a structure similar to that of *grandiflora*.

The culture therefore as a whole was clearly intermediate between the parent species in all of its morphological features but had the anthocyan coloration of *grandiflora*. Such extreme types as were present had the appearance of segregates. Few plants were sufficiently similar to *grandiflora* to justify the expression of their characters whether of foliage, habit or flowers by the formula $(g \times b) \times (b \times g) = g$.

(c) The F_2 generation, *grandiflora* D \times *biennis*, culture 13.41

The second generation from plant 12.48a, F_1 *grandiflora* D \times *biennis*, consisted of 96 plants as the result of a sowing in earth of 459 seeds from 7 capsules, pans kept for 6½-8 weeks, a germination of 20.9 percent. A class of dwarfs (fig. 6) appeared consisting of 22 plants identical with those described for the double reciprocals and these likewise were too weak to live in the garden. There were brought to maturity 74 plants constituting a remarkably uniform assemblage similar to the parent F_1 hybrid type described for culture 12.48 (DAVIS 1914, 193-195). Except for this class of dwarfs there was therefore little evidence of variation in the culture as represented by this small germination of 20.9 percent. In view of my experience with the F_2 generation of the cross *Franciscana* \times *biennis* (DAVIS 1916), where segregation was conspicuous after complete germination, experimentally induced, of 52 percent, I must believe that the uniformity of the healthy plants in this culture

of *grandiflora* \times *biennis* in the F_2 simply means that delayed germination prevented the appearance of more varied types.

(d) The F_2 generation, *biennis* \times *grandiflora* D, culture 13.42

The sowing of 672 seeds from 8 capsules, in earth, parent plant 12.49a F_1 *biennis* \times *grandiflora* D, gave after 6½-8 weeks 59 plants, a germination of 8.7 percent. Of these plants 11 were dwarfs of the type present in the cultures of the double reciprocals, and in the F_2 from *grandiflora* D \times *biennis*; they also died early. This left a culture of 48 plants which matured and these were uniform and similar to the parent F_1 hybrid type described for culture 12.49 (DAVIS 1914, pp. 193-195). A seed germination as low as 8.7 percent indicates that the culture must have been very far from representative of the possibilities of the viable seeds and suggests delayed germination as the reason why there was no greater variation in the culture.

(e) Remarks

One of the most interesting features of these crosses involving *biennis* and *grandiflora* D has been the constant appearance of the same characteristic dwarfs in the relatively large proportions of 18.6-31.7 percent of the totals in the cultures. These are large proportions although the figures can have no genetical significance in view of the low and evidently incomplete germinations obtained from these earth-sown seeds. It is perhaps possible that these peculiar dwarfs with their numerous small leaves and abortive roots (fig. 6) are diseased plants, yet their comparatively uniform structure and large numbers would suggest a genetical reason for their presence. There would seem to me to be every probability that cultures of these and other crosses in which *biennis* and *grandiflora* are concerned would show either unmistakable segregation where germination is experimentally forced to completion, or degrees of sterility that would account for missing classes.

HYBRIDS INVOLVING *OENOTHERA MURICATA* L. AND *OE. GIGAS* DE VRIES

These crosses offer some very interesting problems in cytology and sterility upon which I hope later to make a report. Cultures of the F_1 hybrids in my experience (DAVIS 1914, pp. 197-203) have given similar reciprocals as far as the larger plants were concerned, but narrow-leaved forms are frequently present in the cross *muricata* \times *gigas*, a fact noted also by DE VRIES (1913, p. 181). The F_1 of *muricata* \times *gigas* is not difficult to obtain; germinations in a Petri dish from the contents of 4 capsules (culture 16.30) gave after 5 weeks 11 seedlings and a

residue of 11 large empty seeds, 3 seeds with contents, and a large amount of abortive structures grading into ovule powder. The reciprocal cross *gigas* \times *muricata* yielded an extraordinarily small harvest of viable seeds; the contents of 3 capsules (culture 16.29) gave after 5 weeks in a Petri dish 1 seedling and a residue of 230 large empty seed-like structures. The F_1 hybrids have with one culture excepted (DAVIS 1914, p. 197) proved to be self-sterile both in my experience and in that of DE VRIES. I have made in the past 5 years (1912-1916) 237 attempts to self *muricata* \times *gigas* and 102 attempts to self *gigas* \times *muricata*, all failures. The experiments of 1913, consisting of 75 trials on $m \times g$ and 30 trials on $g \times m$, were with plants heavily fertilized with bone meal, 1 kilogram to the square meter. The behavior of the inter- and back-crosses as far as I have studied them is given below.

(a and b) Double reciprocals

During two seasons (1912, 1916) I have attempted 47 times to make the cross $(g \times m) \times (m \times g)$ and 61 times to make the reverse double reciprocal $(m \times g) \times (g \times m)$ but without results. The hand-pollinated flowers failed to develop a single capsule.

(c) Sesquiereciprocal, *gigas* \times (*muricata* \times *gigas*)

Pollinations of *gigas* from the F_1 *muricata* \times *gigas*, in all 27 operations (1915, 1916), produced no capsules.

(d) Sesquiereciprocal, (*gigas* \times *muricata*) \times *gigas*, culture 17.33

Pollinations in 1916 have given medium-sized capsules well filled with seed-like structures. A culture at date, March 1917, from the contents of 8 capsules in Petri dish presented after 6 weeks 74 seedlings, a germination of about 50 percent. The young rosettes show a wide range of variation and it is probable that the mature culture will exhibit a behavior similar to that described for the iterative $(muricata \times gigas) \times gigas$.

(e) Sesquiereciprocal, *muricata* \times (*gigas* \times *muricata*)

No capsules were produced by this cross, 19 attempts in 1916.

(f) Sesquiereciprocal, (*muricata* \times *gigas*) \times *muricata*, culture 16.32

This cross, 43 trials (1915, 1916), has always yielded full capsules with numerous seed-like structures. Sowings of the contents of 6 capsules in Petri dishes gave in 7-8 weeks 26 seedlings, the residue consisting of 538 empty seeds and 16 with contents; there were also some empty abortive structures and much ovule powder. The germination,

therefore, was very poor, 4.3 percent. The seedlings set in the earth developed no green in their cotyledons and died after 2 or 3 weeks.

(g) Iterative, *gigas* \times (*gigas* \times *muricata*)

This cross produced no capsules, 9 trials in 1916.

(h) Iterative, (*gigas* \times *muricata*) \times *muricata*, culture 17.34

Pollinations in 1916 gave medium-sized capsules well filled with seed-like structures. Only 2 seedlings appeared in a Petri dish culture after 6 weeks, March 1917, from the contents of 10 capsules, about 310 seed-like structures. The germination was therefore extremely low, .64 percent. The 2 seedlings developed no green in their cotyledons and promptly died, thus presenting a behavior similar to that of the sesquiereciprocal (*muricata* \times *gigas*) \times *muricata*.

(i) Iterative, *muricata* \times (*muricata* \times *gigas*)

Pollinations of *muricata* from the F_1 *muricata* \times *gigas* as in the case of the back-cross to the other parent, $g \times (m \times g)$, were fruitless; 61 attempts (1915, 1916) gave no capsules.

(j) Iterative, (*muricata* \times *gigas*) \times *gigas*, culture 16.31

This cross, 56 trials (1915, 1916), always gave well developed capsules with large seeds. From the contents of 3 capsules in a Petri dish there developed after 6 weeks 37 seedlings leaving a residue of 44 empty seeds, 9 seeds with contents, and numerous abortive structures grading into a large amount of ovule powder, a germination of 41 percent. Of the seedlings 36 survived giving a most varied assemblage of plants hardly two of which were alike. This culture was one of the most interesting that I have ever observed among hybrids of *Oenothera*. Evidently there is a very remarkable range in the structure of the female gametes of the F_1 *muricata* \times *gigas* and extended genetical and cytological studies of this back-cross with the *gigas* parent should prove of exceptional interest.

(k) These crosses involving *muricata* and *gigas* so bristle with problems of sterility that discussion of our present data would not be justified. Since the *gigas* parent with 28 chromosomes has double the number present in *muricata*, and the F_1 hybrids are therefore triploid, we may with reason expect that some of the surprising results described above are bound up with irregularities of chromosome distribution.

SUMMARY

1. Data is presented in tables 1 and 2 showing the extent of delayed germination in earth-sown cultures as contrasted with the germination forced to completion under experimental conditions. It is not probable that the cultures here described, being from earth-sown seed, properly represented the possibilities of the viable seeds even though the pans were generally kept for at least 6 weeks.

2. The experimental tests of seed germination in Petri dishes showed some remarkably high degrees of seed sterility especially in the crosses involving *biennis* and *muricata* (table 1).

3. Some new types are added to the forms reported by DE VRIES for the inter- and back-crosses of the F_1 hybrids between *biennis* and *muricata* (page 169). The view is held by the writer that the relatively few types described among these hybrids represent a limited number of classes or segregates able to survive the extraordinarily high mortality among the gametes and zygotes.

4. A much greater variety of forms is found among the inter- and back-crosses of the F_1 hybrids between *biennis* and *Franciscana* where the amount of seed sterility is much less than in the crosses involving *biennis* and *muricata*, and this range of forms is interpreted as segregation.

5. The results for double reciprocals from F_1 hybrids of *biennis* and *grandiflora* also indicate a segregation of factors. Segregation in the F_2 generations from the same F_1 hybrid plants employed in making the double reciprocals was apparently masked by the low percentages of germination obtained from the earth-sown seeds. The presence of a remarkable class of dwarfs (fig. 6) was noted in all of these cultures.

6. Data on crosses involving *muricata* and *gigas* expose remarkable situations with problems of sterility in the foreground.

7. Remarkable linkage or correlations of characters were recorded especially for crosses in which *biennis* and *Franciscana* are concerned.

8. It appears to the writer doubtful whether the formulae presented by DE VRIES for the behavior of the inter- and back-crosses of the F_1 hybrids between *biennis* and *muricata* express a fundamental law. It seems more probable that the results of the formulae represent particular classes among a much larger number which either through delayed germination have not appeared in earth-sown cultures or through high degrees of sterility, both gametic and zygotic, are eliminated.

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FURTHER STUDIES ON THE RELATIONSHIP BETWEEN BILATERAL ASYMMETRY AND FERTILITY AND FECUNDITY IN THE UNILOCULAR FRUIT¹

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INTRODUCTORY

In a paper appearing in an earlier number of GENETICS, I outlined (HARRIS 1916) the attempts which have hitherto been made to solve certain of the problems of the correlation between morphological and physiological characters by the application of quantitative methods to data from plant organisms, and gave series of measurements of degree of development in normal and variant seedlings. In this paper, I shall present the results of the analysis of 16 series of data for fertility in pods of the garden bean. These are supplementary to 53 series already published (HARRIS 1912 a).

While the nature of the problem is fully discussed in the memoir just cited, a simple explanation will serve the reader's convenience.

Externally a bean or pea pod is seen to have two sutures, the dorsal and the ventral. The pod splits most easily along the ventral suture and shows the seeds and the ovules which have ceased development at an early stage to be attached to the two margins just freed by the splitting. These two margins were free in the earlier stages of development. The pod may, therefore, be looked upon as a plate of tissue folded along the dorsal suture about which it is symmetrical or asymmetrical in respect of the number of ovules laid down upon its two margins. If the number be odd (3, 5, 7, etc.) the plate must have one ovule, at least, more on one side than on the other. If the number be even, the organ is most probably symmetrical, for an asymmetrical disposition of the ovules with respect of the central axis could only result from an excess of two ovules on one margin.

If the reader feels inclined to inquire why the discussions of the problem of the relationship of asymmetry and physiological capacity was

¹ Studies on the correlation between morphological and physiological characters. II.

not carried out on materials in which the degree of asymmetry could be expressed on a definite quantitative scale, the answer is very simple. Such measures are very difficult to secure. This is also true of any measure of physiological differentiation. Because of the slightness of variations in these characters and the reasonableness of supposing any relationship between them to be of a low order of magnitude, the number of measurements upon which any conclusion could be based would of necessity be very large indeed. Under these circumstances, it seems most desirable in preliminary work to use observations collected primarily for other purposes. Such data are available for a relatively large number (about a quarter of a million) of pods of garden beans, grown and counted in various genetical studies. Had the analysis of such available materials indicated the absence of any relationship between asymmetry and fecundity, it would be idle to urge the laborious collection of more accurately measured data for the specific purposes of the present problem. In view of the results which we have secured in the preliminary analysis of those collected incidentally, the justification of further studies of the same kind is quite clear.

MATERIALS AND METHODS

The first study of fertility in *Phaseolus* involved the pods secured in 53 cultures of dwarf varieties of garden beans, grown under a wide range of conditions in Kansas, Missouri, Ohio, and on Long Island.

The most comprehensive description of these materials is found in a memoir upon the influence of the starvation of the ascendants upon the characteristics of the descendants, but other information may be secured from a bibliography published elsewhere (HARRIS 1914).

The present investigation is based upon a lot of pods derived from 16 cultures, comprising 4 varieties, made on the grounds of the STATION FOR EXPERIMENTAL EVOLUTION in 1912. These were grown in the same field, hence under conditions of a high degree of uniformity as compared with the first 53 cultures. Details concerning the experimental conditions of this culture will eventually be published elsewhere. The ancestry of the plants and the history of the strains prior to 1912 may be obtained by substituting T for C in the formulae by which the cultures are designated, and referring to an earlier paper (HARRIS 1912 b).

The countings of number of ovules and seeds were made with great care by Miss EDNA LOCKWOOD, Miss MARGARET GAVIN and Miss LILLIE GAVIN, all of whom have had several years' experience in work of this

kind. This phase of the work was, I believe, carried out with greater accuracy than in our preceding series. That the results are altogether trustworthy cannot be urged. The determination of the number of abortive ovules is not always an easy task, and the boundary line between an abortive ovule and a perfectly developed seed is in many cases a purely arbitrary one. There are clear evidences of the existence of personal equation in the countings.

The data are, I believe, quite as accurate (at least) as those upon which genetic conclusions are generally based. They are the best we have been able to obtain up to the present, and have been secured and reduced at the cost of an enormous amount of labor. Until they can be replaced by others demonstrably superior, they may serve their purpose in indicating the nature of certain very obscure relationships. The closeness of agreement of the new data here presented with those due chiefly to other observers is one of the strongest evidences for a degree of accuracy sufficient for present requirements.

The correlation surfaces for number of ovules and number of seeds per pod are shown in the accompanying tables.

		NHHT Series										NHHHT Series							
		Ovules per pod										Ovules per pod							
		3	4	5	6	7	8	9	Totals			3	4	5	6	7	8	9	Tota
Seeds per pod	1	—	—	11	9	2	—	—	22	1	—	3	13	27	8	—	—	—	51
	2	1	8	50	62	19	—	—	140	2	2	14	108	137	53	2	—	—	316
	3	—	9	143	221	61	4	—	438	3	3	43	250	433	116	10	—	—	855
	4	—	23	206	431	120	5	—	785	4	—	51	479	756	213	10	—	—	1509
	5	—	—	266	672	181	9	1	1129	5	—	—	638	1295	324	19	—	—	2276
	6	—	—	—	674	250	14	1	939	6	—	—	—	1461	466	26	—	—	1953
	7	—	—	—	—	230	29	—	259	7	—	—	—	—	424	21	—	—	445
	8	—	—	—	—	—	10	—	10	8	—	—	—	—	—	23	1	—	24
		1	40	676	2069	863	71	2	3722			5	111	1488	4109	1604	111	1	7429

NHDT Series								NHDDT Series								
Ovules per pod								Ovules per pod								
	3	4	5	6	7	8	Totals		3	4	5	6	7	8	9	Totals
1	—	—	5	5	3	—	13	1	—	1	7	18	6	—	—	32
2	1	4	18	34	15	1	73	2	—	13	81	131	27	3	—	255
3	—	7	66	87	39	2	201	3	4	32	193	375	112	6	—	722
4	—	9	102	146	66	5	328	4	—	35	413	693	180	9	—	1330
5	—	—	125	266	68	11	470	5	—	—	535	1163	267	17	1	1983
6	—	—	—	266	125	10	401	6	—	—	—	1328	357	17	—	1702
7	—	—	—	—	87	15	102	7	—	—	—	—	354	15	—	369
8	—	—	—	—	—	12	12	8	—	—	—	—	—	14	1	15
	1	20	316	804	403	56	1600		4	81	1229	3708	1303	81	2	6408

		NDDT Series									NDDDT Series							
		Ovules per pod									Ovules per pod							
		3	4	5	6	7	8	Totals			2	3	4	5	6	7	8	Totals
Seeds per pod	1	---	1	6	5	1	---	13	1	---	---	4	7	13	2	---	---	26
	2	1	3	10	21	1	---	36	2	2	1	4	55	70	16	1	---	149
	3	---	9	54	80	14	---	157	3	---	---	27	141	201	58	1	---	428
	4	---	12	94	138	16	1	261	4	---	---	23	278	397	62	1	---	761
	5	---	---	134	197	22	---	353	5	---	---	---	347	617	88	7	---	1059
	6	---	---	---	248	38	---	286	6	---	---	---	---	778	150	4	---	932
	7	---	---	---	---	44	---	44	7	---	---	---	---	---	140	4	---	144
	8	---	---	---	---	---	1	1	8	---	---	---	---	---	---	2	---	2
		1	25	298	689	136	2	1151			2	1	58	828	2076	516	20	3501

NDHT Series

Ovules per pod

		3	4	5	6	7	8	9	Totals
Seeds per pod	1	—	3	8	7	1	—	—	19
	2	1	4	35	67	14	—	—	121
	3	2	23	102	150	37	2	—	316
	4	—	17	220	268	54	3	1	563
	5	—	—	274	427	72	2	—	775
	6	—	—	—	546	82	4	—	632
	7	—	—	—	—	86	4	—	90
		3	47	639	1465	346	15	1	2516

NDHHT Series

Ovules per pod

	3	4	5	6	7	8	Totals
1	—	1	8	7	5	—	21
2	1	9	49	73	11	1	144
3	—	18	135	183	42	4	382
4	—	34	288	373	68	4	767
5	—	—	395	633	86	3	1117
6	—	—	—	755	104	5	864
7	—	—	—	—	107	7	114
8	—	—	—	—	—	3	3
	1	62	875	2024	423	27	3412

USHT Series

Ovules per pod

Seeds per pod							Totals
	3	4	5	6	7	8	
1	1	16	56	77	13	—	163
2	5	13	144	162	21	—	345
3	3	45	231	272	35	—	586
4	—	43	411	369	45	1	869
5	—	—	467	549	72	—	1088
6	—	—	—	590	71	2	663
7	—	—	—	—	52	3	55
8	—	—	—	—	—	3	3
	9	117	1309	2019	309	9	3772

USHHT Series

Ovules per pod

Seeds per pod							Totals
	3	4	5	6	7	8	
1	2	10	44	47	9	—	112
2	4	17	110	141	18	—	290
3	1	28	158	233	34	1	455
4	—	26	308	307	30	2	673
5	—	—	418	503	40	1	962
6	—	—	—	490	55	—	545
7	—	—	—	—	48	2	50
	7	81	1038	1721	234	6	3087

USDT Series
Ovules per pod

	3	4	5	6	7	8	Totals
1	2	8	63	51	5	—	129
2	7	8	110	130	20	—	275
3	2	48	151	146	28	—	375
4	—	44	299	240	22	—	605
5	—	—	425	335	33	1	794
6	—	—	—	347	38	—	385
7	—	—	—	—	37	1	38
	11	108	1048	1249	183	2	2601

USDDT Series
Ovules per pod

	2	3	4	5	6	7	8	Totals
1	—	1	11	59	77	8	—	156
2	1	8	25	144	209	32	—	419
3	—	4	62	269	293	50	2	680
4	—	—	65	447	464	45	—	1021
5	—	—	—	533	689	71	—	1293
6	—	—	—	—	642	69	—	711
7	—	—	—	—	—	75	—	75
	1	13	163	1452	2374	350	2	4355

FSHT Series
Ovules per pod

	4	5	6	7	8	Totals
1	1	27	42	24	2	96
2	2	53	137	63	3	258
3	8	88	219	115	6	436
4	12	126	322	163	7	630
5	—	145	451	185	8	789
6	—	—	508	200	7	715
7	—	—	—	188	9	197
8	—	—	—	—	6	6
	23	439	1679	938	48	3127

FSHHT Series
Ovules per pod

	3	4	5	6	7	8	9	Totals
1	—	2	20	39	31	1	—	93
2	1	1	53	137	90	4	—	286
3	1	8	68	270	142	13	—	502
4	—	2	134	327	190	6	—	659
5	—	—	204	600	230	12	—	1046
6	—	—	—	562	269	8	—	839
7	—	—	—	—	244	17	—	261
8	—	—	—	—	—	13	—	13
9	—	—	—	—	—	—	1	1
	2	13	479	1935	1196	74	1	3700

FSDT Series										FSDDT Series									
Ovules per pod										Ovules per pod									
3 4 5 6 7 8 9 Totals										2 3 4 5 6 7 8 9 Totals									
Seeds per pod	1	1	2	15	30	11	1	—	60	1	1	—	1	16	35	19	—	—	72
	2	1	6	41	122	60	7	—	237	2	—	—	6	57	125	61	3	—	252
	3	—	5	80	171	100	7	—	363	3	—	—	11	80	231	119	10	—	451
	4	—	4	96	244	117	13	—	474	4	—	—	10	155	377	145	8	—	695
	5	—	—	107	335	152	13	—	607	5	—	—	—	231	604	217	8	—	1060
	6	—	—	—	377	192	16	1	586	6	—	—	—	—	693	268	11	—	972
	7	—	—	—	—	185	12	—	197	7	—	—	—	—	—	260	17	1	278
	8	—	—	—	—	—	7	—	7	8	—	—	—	—	—	—	6	—	6
2 17 339 1279 817 76 1 2531										1 — 28 539 2065 1089 63 1 3786									

Two methods of comparing the capacity for seed production of asymmetrical ("odd") and probably symmetrical ("even") pods have been employed. First, the simple ratios of the total number of seeds matured to the total number of ovules laid down has been computed for both types of pod. In comparison, $F_o - F_e$ gives the sign and the magnitude of the difference in the two coefficients of fertility. Thus for series NHHHT the results are:

$$\begin{aligned}
 &\text{For "odd" pods, total ovules} = 18692, \\
 &\quad \text{total seeds} = 14804, \\
 &\quad 14804/18692 = .79199 = F_o \\
 &\text{For "even" pods, total ovules} = 25986, \\
 &\quad \text{total seeds} = 20885, \\
 &\quad 20885/25986 = .80370 = F_e \\
 &F_o - F_e = .79199 - .80370 = -.01171
 \end{aligned}$$

Second, the average deviations of the empirical mean number of seeds matured for each number of ovules formed per pod from the theoretical mean number due to a regression equation based on the whole population has been computed for both "odd" and "even" pods, as they will be called for the sake of convenience.

The only problem to be solved in the use of this method is the selection of the regression equation to be employed. Because of its very

general validity and the ease with which it may be computed, the straight line equation

$$s = (\bar{s} - r_{os} \frac{\sigma_s}{\sigma_o} \bar{o}) + r_{os} \frac{\sigma_s}{\sigma_o} o$$

where the bars denote means and the sigmas the standard deviations of the two variables, o = ovules and s = seeds per pod whose correlation is measured by r , must first be tested.

As in the first paper, the linear equation is the only one used.

To meet the possibility that there may be geneticists unfamiliar with the arithmetical processes employed, they may be illustrated on series NHHHT.

The correlation coefficients may be most advantageously determined by a method giving the total number of seeds produced by pods of each ovule grade (HARRIS 1910). Thus:

Ovules per pod	Number of pods	Total seeds in pods
3	5	13
4	111	364
5	1488	6085
6	4109	19865
7	1604	8698
8	111	656
9	1	8

$$N = 7429, \quad \Sigma(os) = 217316, \quad \Sigma(os)/N = 29.252385$$

For ovules:

$$\begin{aligned} \Sigma(o) &= 44678, & \Sigma(o)/N &= 6.013998, & \mu_2 &= .542820 \\ \Sigma(o^2) &= 272726, & \Sigma(o^2)/N &= 36.710992, & \sigma_o &= .736763 \end{aligned}$$

For seeds:

$$\begin{aligned} \Sigma(s) &= 35689, & \Sigma(s)/N &= 4.804010, & \mu_2 &= 1.649307 \\ \Sigma(s^2) &= 183703, & \Sigma(s^2)/N &= 24.727819, & \sigma_s &= 1.284253 \end{aligned}$$

Whence

$$r_{os} = \frac{\Sigma(os)/N - o\bar{s}}{\sigma_o \sigma_s} = \frac{29.252385 - 6.013998 \times 4.804010}{.736763 \times 1.284253} = .381613$$

In terms of regression we have

$$s = (\bar{s} - r \frac{\sigma_s}{\sigma_o} \bar{o}) + r \frac{\sigma_s}{\sigma_o} o$$

or, substituting constants,

$$s (= 4.804010 - .381613 \frac{1.284253}{.736763} 6.013988) + .381613 \frac{1.284253}{.736763} o$$

the final result is

$$s = .803558 + .665190 o$$

For the calculation of η we have

Ovules per pod	Number of pods	$\bar{s}_r - s$	$(\bar{s}_r - s)^2$
3	5	-2.20401	4.85766
4	111	-1.52473	2.32480
5	1488	-.71463	.51069
6	4109	+.03050	.00093
7	1604	+.61868	.38277
8	111	+1.10590	1.22301
9	1	+3.19599	10.21435

$$s [n_x (\bar{s}_r - s)^2] = 1806.00073$$

$$\eta^2 = \frac{s [n_x (\bar{s}_r - s)^2] / N}{\sigma_s^2} = \frac{.243101}{1.649307}, \eta = .3839$$

BLAKEMAN'S (1906) test is given by

$$\eta^2 - r^2 = .001767, \quad 1 - \eta^2 - r^2 = 1 - \zeta = .042043$$

whence

$$\frac{1}{2} \frac{1 - \zeta}{\chi_1} = 2.686$$

Calculating the theoretical or smoothed means from the regression equations

$$s = .803558 + .665190 o$$

and comparing with the empirical means

Ovules per pod	Number of pods	Average seeds \bar{s}_r	Calculated average seeds \bar{s}_r'	Average seeds less calculated average seeds $\bar{s}_r - \bar{s}_r'$
3	5	2.60000	2.79913	-.19913
4	111	3.27928	3.46432	-.18504
5	1488	4.08938	4.12951	-.04013
6	4109	4.83451	4.79470	+.03981
7	1604	5.42269	5.45989	-.03720
8	111	5.90991	6.12508	-.21517
9	1	8.00000	6.79027	+1.20973

Summing the product of the deviations of these empirical means from the theoretical straight lines due to the equations by the numbers of pods upon which they are based, I find

For even pods, $+119.16031$,

For odd pods, -119.15566 .

or since there are 3098 odd pods the mean deviation of the asymmetrical class is

$-.0384$

RESULTS

The accompanying table contains the fundamental constants upon which discussions must be based.

The magnitude of the relationship between the number of ovules formed and the number of seeds developing per pod is shown by the correlation coefficients in the first column, by the correlation ratios in the second column, and by the second constant of the regression straight line equations in the fourth column following the key letters. The closeness of agreement of the several series is shown by the regression lines which have been drawn for all the series in diagram 1.

Consider first of all the nature of the change in the mean number of seeds matured per pod associated with variations in the number of ovules per pod.

The distribution of the empirical means around the regression straight line is shown for four of the series in diagram 2.

The ratio of $\frac{1}{2} \sqrt{\chi^2}$ of BLAKEMAN'S test for linearity (BLAKEMAN 1906) to the χ_1 of Miss GIBSON'S tables (1906) appears in the third column of the table.

To be considered as indicating strictly linear regression, i.e., a uniform rate of change in mean number of seeds per pod, the value of $\frac{1}{2} \sqrt{\chi^2} / \chi_1$ should not exceed 2.5. The entries in the third column show that it does as a matter of fact exceed this value in 13 out of the 16 cases.

Thus regression cannot, by formal tests, be considered linear. Two points must, however, be taken into account. First, if there be a relationship between the bilateral asymmetry of the ovary and its capacity for maturing its ovules into seeds, strictly linear regression cannot obtain. Second, one single type of equation is desirable for comparative studies,—at least, for those of a preliminary nature. Since the straight line equation was the one employed in the first series of determinations

Series	Coefficient of correlation, r	Correlation ratio, η	$\frac{1}{2} \sqrt{\frac{r}{\chi_1}}$	Regression equation	Mean deviation of odd	$F_o - F_s$
HHT	.4177	.4195	1.757	$s = + .3863 + .7301 \ o$	-.0421	-.01281
HHHT	.3816	.3839	2.686	$s = + .8035 + .6651 \ o$	-.0384	-.01171
HDT	.3818	.3873	1.919	$s = + .8884 + .6373 \ o$	-.0882	-.02558
HDDT	.3624	.3657	2.896	$s = + .9608 + .6413 \ o$	-.0304	-.00909
DDT	.3814	.3825	7.142	$s = + .5519 + .7112 \ o$	+.0274	+.01290
DDDT	.3677	.4466	11.120	$s = + .7797 + .6712 \ o$	-.0665	-.01408
DHT	.3307	.3435	3.462	$s = + 1.1866 + .5954 \ o$	-.0730	-.01182
DHHT	.3343	.3445	3.599	$s = + 1.2441 + .5950 \ o$	-.0885	-.01309
USHT	.2943	.3019	3.046	$s = + .7972 + .6034 \ o$	-.0258	+.00521
USHHT	.2760	.2860	3.086	$s = + .9933 + .5763 \ o$	-.0091	+.01484
USDT	.2597	.2648	1.963	$s = + 1.2248 + .5231 \ o$	-.0018	+.02189
USDDT	.2818	.2877	2.844	$s = + 1.0344 + .5023 \ o$	-.0153	+.01170
FSHT	.2489	.2590	2.960	$s = + 1.2488 + .5280 \ o$	-.0956	-.03840
FSHHT	.2274	.2357	2.808	$s = + 1.6355 + .4757 \ o$	-.0625	-.03364
FSDT	.2937	.3030	2.777	$s = + .7971 + .6012 \ o$	-.0170	-.01164
FSDDT	.2744	.2808	2.710	$s = + 1.3101 + .5517 \ o$	-.0546	-.02605

it seems desirable to use it here as well, especially in view of the fact that it is not yet demonstrated that any other single equation would prove more effective in smoothing the empirical means.²

Turn now to the two measures of the capacity of the two types of pods for seed production. These are given in the two final columns of the table.

In presenting these results I shall first give those derived from the sixteen new experiments, here presented for the first time. I shall then combine with these the fifty-three series already published. Thus the present paper not only forms a contribution of a large mass of new material, but summarizes the whole of the available data.

Considering the signs only of the constants measuring the relationship between asymmetry and capacity for seed production, it is clear that with a single exception the regression line method indicates lower fertility in the asymmetrical pods. The results are not so concordant in the case of the method of differences in coefficients of fertility, for here 5 out of the 16 series show a lower fecundity in the more symmetrical class of pods.

² The actual data are published and at the disposal of anyone who feels inclined to fit regression curves of a higher order. Personally, I feel that the time required would be better employed on the biological rather than the statistical side of the problem.

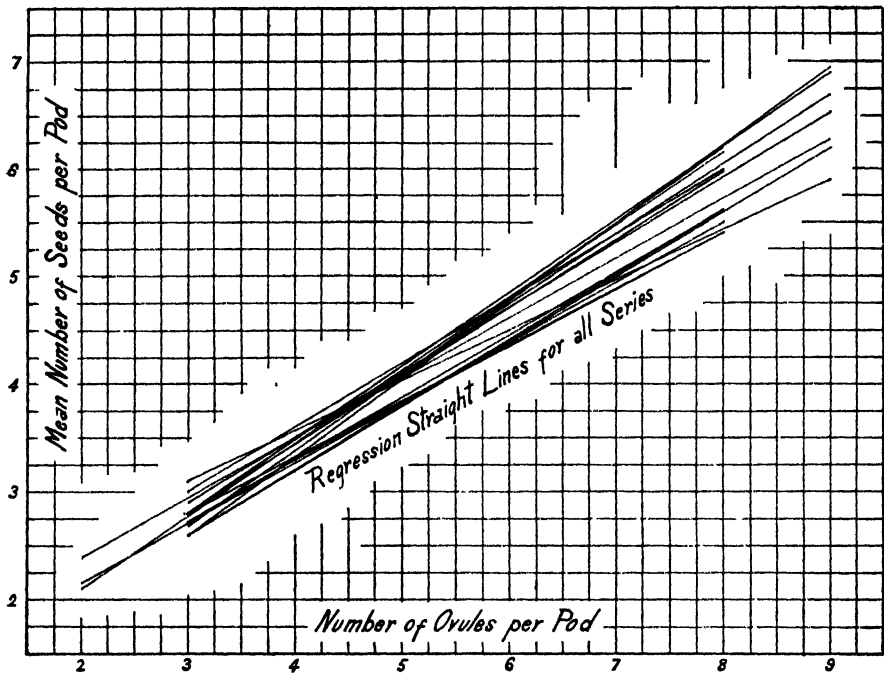


DIAGRAM 1.—Straight lines showing the regression of number of seeds matured upon number of ovules formed per pod in 16 cultures of *Phaseolus*.

In the sets of observations already published there were by both methods 35 series in which the asymmetrical pods showed a lower capacity for maturing their ovules into seeds as compared with 18 in which they showed a higher capacity. This comparison is of course based on signs only. An analysis of the results on the basis of the magnitudes of the coefficients will be made presently.

Considering all the constants available up to the present time, it is clear that as analyzed by the regression line method there are 50 series in which the asymmetrical pods show a smaller capacity for maturing their ovules into seeds as compared with 19 in which they show a higher capacity. If conclusions be drawn from the coefficient of fecundity method, the results are in practical agreement. Thus 46 of the 69 series show a lower capacity for maturing ovules into seeds in the asymmetrical pods.

These are rather wide deviations from the equality which one would expect if there were no biological cause for differences in the fertility of the two classes of pods, i. e., if the differences observed were due purely and simply to the probable errors of random sampling. If such

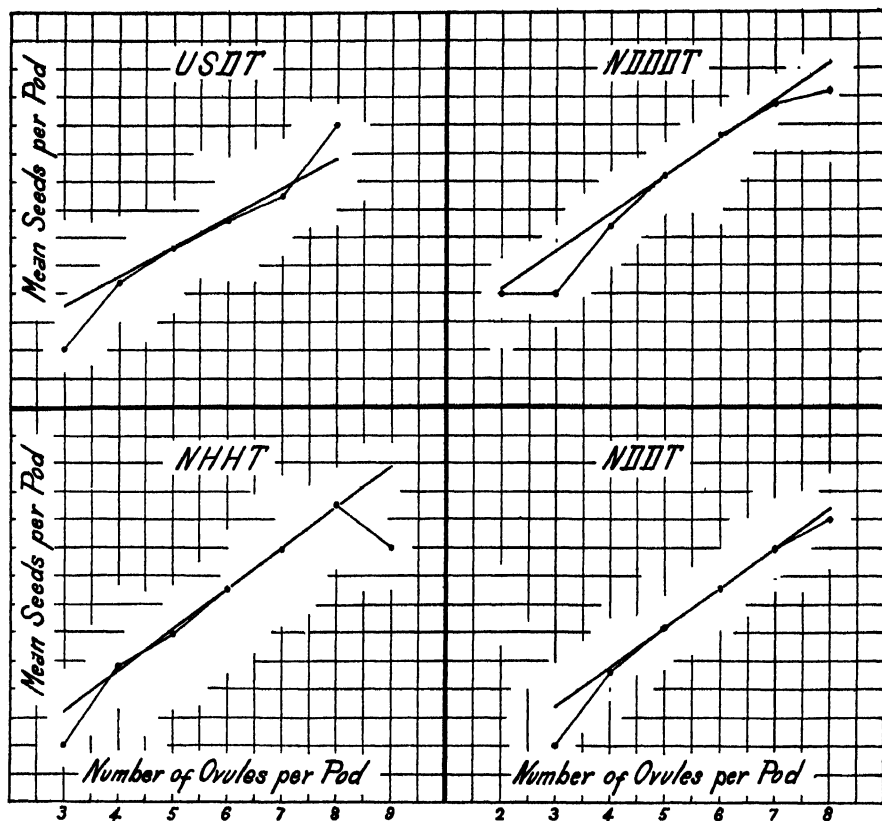


DIAGRAM 2.—Regression straight lines with empirical mean numbers of seeds per pod in four series of *Phaseolus*.

were the origin of the observed differences in the fecundity of the two classes of pods, there should be, within the limits set by the probable error of random sampling given by

$$.67449\sqrt{69 \times .5 \times .5}$$

an equal division into two groups in one of which the symmetrical and in the other of which the asymmetrical is the more fertile. The actual deviation of the observed number of positive and negative coefficients from equality is,

For the regression line method

$$50 - 34.5 = 15.5 \pm 2.80$$

For the coefficient of fertility method

$$46 - 34.5 = 11.5 \pm 2.80$$

These deviations from equality are about 5.5 and 4.1 times as large as

their probable errors and must, therefore, be looked upon as probably significant.

The results by the regression line method are so uniform throughout that it is difficult to discuss the closeness of agreement of this and the coefficient of fecundity method on the new materials. Combining the present series with those previously published, we have the results set forth in the accompanying table.

Coefficient of fertility method

Regression line method		+	—	Totals
	+	15	4	19
	—	8	42	50
	Totals	23	46	69

Thus the two methods, which do not necessarily give identical results, are in very close agreement indeed. Series which are classified as showing a negative relationship by one method will in the great majority of instances—in 57 of the 69 available cases—show the same relationship when classified by the other method. Were the two methods employed not thus consistent, no confidence whatever could be placed in the results. That they are not in universal agreement is due to the fact that no single method of analyzing the data so far known is without some objectionable feature.

A comparison of the two methods of determining the relationship between bilateral asymmetry and the capacity of the ovary for maturing its ovules into seeds, which takes into account the magnitudes of the constants, instead of their signs merely, may best be made by determining the correlation between them. This is found to be

$$r = .8577,$$

a value indicating a very close agreement indeed. The relationship is represented graphically in diagram 3 in which the closeness of agreement is shown by the slope of a straight line representing the regression equation deduced from the correlation coefficient. The solid dots show the position with reference to the two general means and the regression straight line of both constants for the 69 individual series. The shaded areas show the magnitude of the deviation of the two general means for the two methods of measurement from the zero which would be

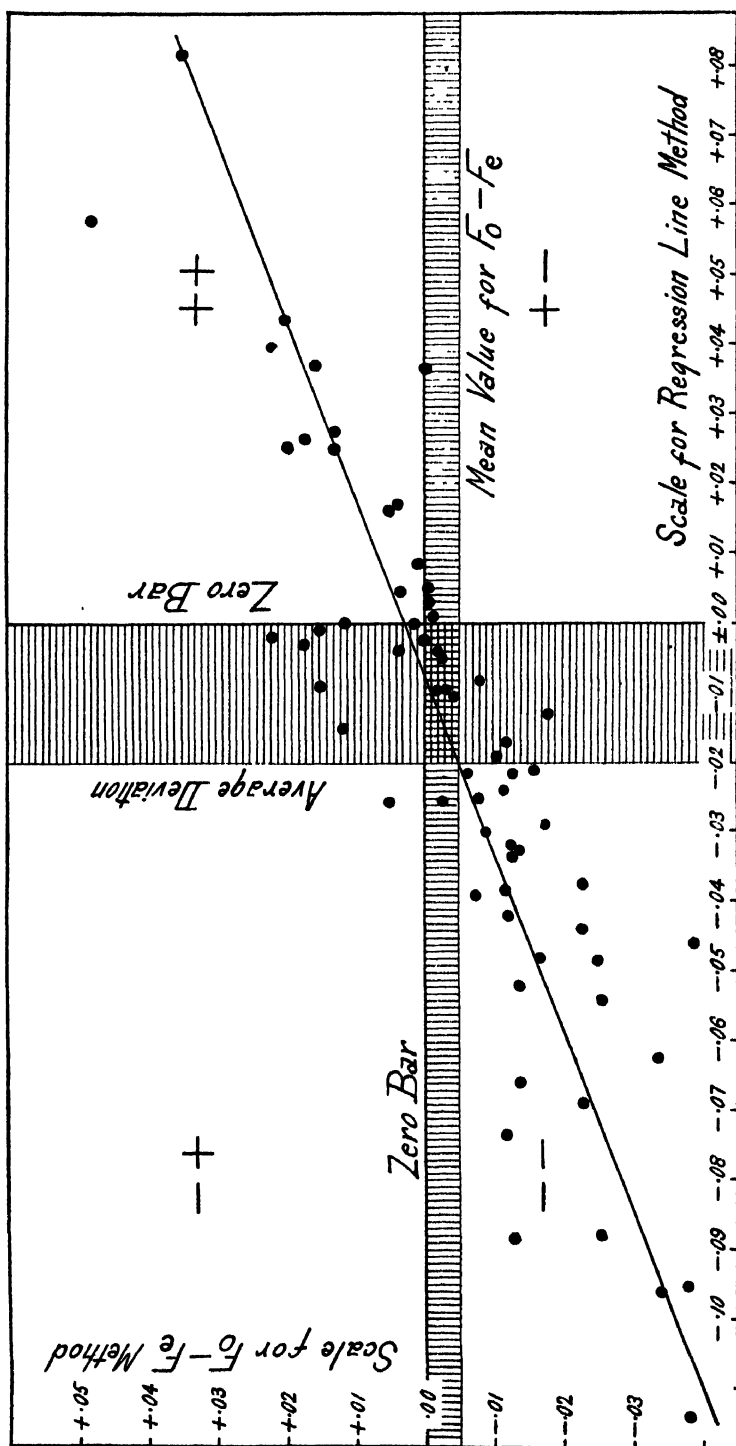


DIAGRAM 3.—Scatter diagram showing the agreement between the two methods used in computing the capacity for seed production of symmetrical and asymmetrical pods. The solid dots show on the two scales the actual values obtained by the two methods. The shaded areas show the extent of the deviations of the means of the two sets of results from zero. The straight line represents, in terms of regression, the correlation between the results of the two methods.

expected as the average of the constants if there were no difference in the capacity of the two types of pods for maturing their ovules into seeds.

One of the strongest evidences for the validity of the conclusions concerning a negative relationship between bilateral asymmetry with respect of ovule number and capacity for seed production is the consistency of results obtained at different times with series of materials which in many ways are quite dissimilar. The results have been worked up in four lots as the data have accumulated. These series have been counted, tabled and analyzed at periods several years apart. Classifying the data into these purely arbitrary groups, the results for the signs of the coefficients measuring the capacity for seed production of asymmetrical pods are as follows:

By the regression line method:

- Lot 1. 20 series, 15 negative and 5 positive.
- Lot 2. 20 series, 12 negative and 8 positive.
- Lot 3. 13 series, 8 negative and 5 positive.
- Lot 4. 16 series, 15 negative and 1 positive.

By the method of comparison of coefficients of fecundity:

- Lot 1. 20 series, 14 negative and 6 positive.
- Lot 2. 20 series, 12 negative and 8 positive.
- Lot 3. 13 series, 9 negative and 4 positive.
- Lot 4. 16 series, 11 negative and 5 positive.

Such uniformity of results can hardly be due to chance. It indicates the existence of a real biological relationship between asymmetry and capacity for seed production.

Series	Regression line method		$F_a - F_c$ method		Totals
	Negative	Positive	Negative	Positive	
Navy (H)	9	4	10	3	13
Navy (D)	9	4	10	3	13
Burpee's Stringless (G)	5	3	6	2	8
Ne Plus Ultra (U)	10	5	3	12	15
White Flageolet (F)	14	1	14	1	15
Golden Wax (L)	3	0	3	0	3
Black Wax (BW)	0	2	0	2	2
Totals	50	19	46	23	69

As another check upon our conclusions, the constants for all available series may be classified by varieties, as in the table immediately above.

Note that in every variety with the exception of Ne Plus Ultra and Black Wax (in which the materials were very unsatisfactory) the relationships are of the same general kind.

Turning to averages as a means of closer analysis, I find the following results for the 16 new series. The constants obtained from the 53 series investigated some years ago are added for comparison and the averages based on all the available data are laid beside the others.

Regression line method,

New series	— .0426
Earlier series	— .0139
All series	— .0202

Coefficient of fecundity method,

New series	— .0088
Earlier series	— .0040
All series	— .0051

If instead of giving the constants for the 69 series equal weight in determining their average value, they be loaded with the number of asymmetrical pods upon which they are based, the results are as follows:

Regression line method,

New series	— .0428
Earlier series	— .0125
All series	— .0191

Coefficient of fecundity method,

New series	— .0096
Earlier series	— .0037
All series	— .0050

Thus the average values of the constants, as well as the distribution with regard to signs, indicate a lower capacity for seed development in the bilaterally asymmetrical pods.

By both methods the magnitudes of the differences are larger in the second series of determinations than they are in the first. This is the result which one would expect if there be a negative relationship between asymmetry and capacity for seed production and if the second series of determinations is technically the better of the two.

The question naturally arises: Why, if there be really a negative relationship between morphological asymmetry and physiological capacity, do a certain number of the coefficients show a positive correlation between these two variables, i. e., indicate that the asymmetrical pods are more capable of carrying out their physiological functions than the symmetrical?

There may be biological factors not yet fully investigated underlying this phenomenon, but I think it is due chiefly to the slightness of the relationship under investigation and the difficulty of obtaining samples of data adequately large and sufficiently free from error to demonstrate the general law in each individual instance. For two reasons large differences should not be expected between the fertility of symmetrical and asymmetrical ovaries. First, the actually existing asymmetry in these cases is not large. Second, the correlation between somatic characters and fertility is (as I have shown in papers which need not be cited here) generally low.

In such delicate interdependencies, there is always the possibility that the errors of sampling may give even a false sign to a constant based upon samples of the size that one is ordinarily able to secure in biological work. In any series of determinations one must, therefore, expect a number of the constants to bear positive signs, even though the actual biological relationship in an infinitely large population may be a negative one.

RECAPITULATION

The foregoing pages present the results of the statistical reduction of data bearing on the problem of the relationship between bilateral asymmetry with respect of number of ovules produced on the two carpellary margins and the capacity for seed production of the unilocular fruit.

Primarily, they set forth the constants derived from the data of 16 hitherto unanalyzed series of garden beans, comprising a total of 56698 pods. Secondly, they give the results of comparison and combination with the constants from 53 series comprising 166130 pods published in 1912.

The constants of either of these lots of data taken independently may be considered to establish the conclusion that there is a negative relationship between bilateral asymmetry and the capacity of the pod for maturing its ovules into seeds.

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ON THE APPLICABILITY OF PEARSON'S BISERIAL r TO THE PROBLEM OF ASYMMETRY AND FERTILITY IN THE UNILOCLAR FRUIT

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INTRODUCTORY

When PEARSON (1909) published his formula for measuring the intensity of relationship between an alternative and a quantitatively measured variable, it was quite clear that the method might be used in certain problems of fertility and fecundity which had then been under investigation for several years. In preparing a first paper on these studies (HARRIS 1912) it seemed desirable to forego the application of correlation methods to the problem until the formula had been somewhat more widely tested in practical work. The present paper proposes to illustrate the applicability of this method, unfortunately little used by biologists, to the problem of the relationship between bilateral asymmetry and capacity for seed production in the unilocular fruit.

Beyond any value which it may have as indicating biological applications for a valuable but as yet little recognized formula, the paper is solely a contribution to the further analysis of data presented elsewhere (HARRIS 1912, 1917 a).

It may be said at the outset that while correlation formulae are not essential for the demonstration of the existence of relationships of the kind under investigation, their application does allow of the measurement of the intensity of the interrelationship on a quantitative scale. Their use marks, therefore, the transition from relatively qualitative to relatively quantitative work.

METHODS

The method of analysis here employed is in essence very simple. Let r_{ao} be the correlation between asymmetry and number of ovules laid down, r_{as} the correlation between asymmetry and number of seeds matured. Now the values of r_{as} will be to some extent influenced by

¹ Studies on the correlation between morphological and physiological characters. III.

these of r_{ao} , since r_{os} , the correlation between number of ovules and number of seeds per pod, has always (in *Phaseolus*) been found to have a substantial positive value. To obtain a measure of the correlation between asymmetry and number of seeds produced *free from the influence of the correlation between asymmetry and number of ovules*, the well known partial correlation formula for three variables has been employed.

The only assumption necessary in the application of the biserial r is that the alternative character is *normal* in its frequency distribution. While asymmetrical and symmetrical, as measured by the "odd" or "even" number of ovules formed, must formally be regarded as truly discontinuous, they cannot be so considered fundamentally. Number of ovules while nominally a discrete variate is in reality dependent upon a large number of antecedent proximate causes, physiological and morphological, which are essentially continuous in their influence. Whether these shall produce an odd or an even number of ovules depends in all probability upon purely quantitative differences in the weight of these factors. For the great majority of practical purposes such variations may be considered to follow the normal or Laplace-Gaussian law.

Thus all that we require for the expression of the results for the 69 series of *Phaseolus* for which data on the number of ovules formed and the number of seeds matured per pod are now available, on as nearly as possible a truly quantitative scale is the 138 correlation coefficients for asymmetry and ovule and seed numbers, the 69 correlation coefficients for number of ovules and seeds, and the 69 partial correlations between asymmetry and number of seeds for constant number of ovules per pod.

It may be useful to illustrate the processes. In the simple formulae

$$r_{ao} = \frac{(\bar{o}_a - \bar{o})/\sigma_o}{s/f}, \quad r_{as} = \frac{(\bar{s}_a - \bar{s})/\sigma_s}{s/f}$$

\bar{o}_a , \bar{s}_a indicate the mean number of ovules and seeds in asymmetrical pods, \bar{o} , \bar{s} , the mean number of ovules and seeds in all pods, σ_o , σ_s the standard deviations of number of ovules and seeds in the population at large. Thus the evaluation of the numerator is very simple indeed, consisting merely in the determination of the ratio of the deviation of the mean of the selected class from the population mean to the population standard deviation. Note that the sign of the correlation coefficient is given at once by $\bar{o}_a - \bar{o}$, $\bar{s}_a - \bar{s}$.

The value of the denominator must be determined from SHEPPARD'S tables of the probability integral (SHEPPARD 1902).

The necessary constants may be obtained in either of two ways. An illustration of the actual arithmetic may be useful to those who would like to follow the work in detail.

For series NHHHT

$$\frac{1}{2}(1-a) = 3098/7429 = .4170144$$

$$\frac{1}{2}(1+a) = 4331/7429 = .5829856$$

$$a = .1659712$$

SHEPPARD'S tables I-II (II of PEARSON'S volume) give for the lower value of $\frac{1}{2}(1+a)$

$$\frac{1}{2}(1+a) = .5792597, \Delta = .0039065$$

Hence

$$\theta = (.5829856 - .5792597) / .0039065 = .95377$$

$$\theta(1-\theta)/2! = .04409$$

The values of z corresponding to $\frac{1}{2}(1+a) = .5792597$ in SHEPPARD'S tables are

$$z = .3910427, \Delta = .0008008, \Delta^2 = .0000373$$

Whence by the advancing difference formula

$$u = u_0 + \theta \Delta u_0 - \frac{\theta(1-\theta)}{2!} \Delta^2 u_0$$

$$z = .3910427 - (.95377 \times .0008008) + (.02205 \times .0000373) = .3902797$$

Using table III we have

$$a = .16, z = .3908939, \Delta = .0010415, \Delta^2 = .0000641$$

$$\theta = .59712, \frac{\theta(1-\theta)}{2!} = .12028$$

Whence by the advancing difference formula

$$z = .3908939 - (.59712 \times .0010415) + (.12028 \times .0000641) = .3902796$$

a value differing by only 1×10^{-7} from that derived from SHEPPARD'S tables I-II, notwithstanding the small number of decimals retained in clearing the formulae.

RESULTS

The values of r_{os} , r_{ao} , and r_{as} , which are essential for the determination of the partial correlations between asymmetry and number of seeds matured for constant numbers of ovules per pod, are given in the first three columns of the accompanying table.

The values of r_{os} are treated in sufficient detail in a forthcoming paper (HARRIS 1917 b). Researches which may facilitate the interpretation of

the values of r_{ao} and r_{as} are still in progress. They will not, therefore, be discussed in this paper, further than to point out that both are preponderantly negative in sign, i. e., that as a rule a lower number of both ovules and seeds is associated with asymmetry.

The values of ${}_or_{as}$ are distributed between positive and negative in the ratio 19 : 50. Thus they show a deviation of 15.5 ± 2.80 from an equality of division into positive and negative coefficients. Since the number of negative partial correlation coefficients is distinctly greater than the number of positive ones, the asymmetrical pods are relatively as well as absolutely less fertile than the symmetrical ones.

The values of ${}_or_{aa}$ are generally low. They range from $-.0996$ to $+.0817$, with a general average of $-.0185$. The average for the 19 positive partial correlations is $+.0269$ as compared with $-.0358$ for the 50 negative coefficients. Thus there is not merely a negative general average, but the average magnitude of the coefficients which are negative in sign is numerically larger than that of those which are positive in sign.

The results may now be compared with those secured in the other

Series	r_{or}	r_{ao}	r_{as}	${}_or_{as}$
L	.3740	-.0254	-.0204	-.0118
LL	.3567	-.1032	-.0717	-.0030
LG	.1070	+.2373	-.0321	-.0595
BW	.1766	-.0327	+.0746	+.0817
BW ₂	.1281	-.0286	+.0395	+.0435
G	.5420	-.0106	-.0313	-.0303
GG	.2460	-.0163	-.0221	-.0187
GGH	.4611	-.0301	-.0237	-.0110
GGH ₂	.5167	-.1173	-.0559	+.0055
GGHH	.4891	-.1265	-.0901	-.0326
GGD	.3616	+.0952	+.0390	+.0050
GGD ₂	.4257	-.0388	-.0503	-.0374
GGDD	.3863	+.1547	+.0996	+.0439
H	.4444	-.3451	-.1394	-.0167
HH	.5109	-.2781	-.1420	+.0002
HHC	.5037	-.3212	-.1286	+.0405
HHT	.4177	+.0806	-.0013	-.0387
HHH	.4257	-.3780	-.1882	-.0325
HHHC	.5007	-.2505	-.1429	-.0208
HHHT	.3816	+.0284	-.0212	-.0346
HD	.4178	+.1444	+.0766	+.0181
HDC	.5094	-.2518	-.1677	-.0474
HDT	.3819	+.0273	-.0605	-.0768

Series	r_{or}	r_{ou}	r_{as}	or_{as}
HDD	.4999	-.0116	-.0119	-.0070
HDDC	.4635	-.4016	-.1994	-.0163
HDDT	.3625	+.0234	-.0164	-.0267
D	.5214	-.0075	-.0335	-.0346
DD	.4963	+.2423	+.1118	-.0100
DDC	.4633	-.4944	-.2279	+.0015
DDT	.3815	-.2921	-.0895	+.0248
DDD	.4437	+.3536	+.1608	+.0046
DDDC	.4292	-.4401	-.2362	-.0582
DDDT	.3678	-.1761	-.1182	-.0637
DH	.5476	-.2571	-.1315	+.0114
DHC	.4004	-.4939	-.2244	-.0280
DHT	.3307	-.2324	-.1370	-.0655
DHH	.4462	-.3183	-.1466	-.0054
DHHC	.4375	-.4420	-.2333	-.0404
DHHT	.3343	-.2882	-.1694	-.0809
USC	.3309	-.5046	-.1665	+.0007
USS	.5050	-.2408	-.1384	-.0194
USSC	.3310	-.4800	-.1366	+.0274
USH	.4700	-.1736	-.0552	+.0209
USHC	.3224	-.4644	-.1510	+.0014
USHT	.2044	-.4802	-.1614	-.0240
USHH	.3658	-.4046	-.1192	+.0310
USHHC	.3182	-.3697	-.1417	-.0273
USHHT	.2761	-.5244	-.1517	-.0085
USD	.3762	+.0140	-.0224	-.0290
USDC	.2447	-.4542	-.0559	+.0640
USDT	.2597	-.5031	-.1322	-.0018
USDD	.3697	+.1834	+.0310	-.0302
USDDC	.3153	-.4512	-.1453	-.0036
USDDT	.2818	-.4487	-.1383	-.0138
FSC	.3444	+.1691	+.0017	-.0611
FSS	.3672	-.0041	-.0423	-.0139
FSSC	.4115	+.1689	+.0264	-.0480
FSH	.4580	-.3819	-.1832	-.0100
FSHC	.2684	+.0706	-.0650	-.0874
FSHT	.2490	+.2948	+.0024	-.0767
FSHH	.3982	-.5785	-.2653	-.0466
FSHHC	.3247	+.0086	-.0629	-.0694
FSHHT	.2274	+.3221	+.0247	-.0527
FSD	.4332	-.0465	-.0242	-.0046
FSDC	.2665	+.0625	-.0791	-.0996
FSDT	.2937	+.2700	+.0667	-.0139
FSDD	.4212	-.0633	+.0287	+.0612
FSDDC	.3284	+.0237	-.0596	-.0714
FSDDT	.2745	+.2710	+.0325	-.0452

two methods of analysis. This may be most conveniently done by means of the correlation coefficient.

The results are:

For r_{as} and $F_o - F_e$ method

$$r = .850 \pm .023$$

For r_{as} and mean deviation from regression straight line method

$$r = .986 \pm .002$$

The straight line regression equation is shown for the mean deviation method and the r_{as} method in diagram 1. Here the actual constants secured by the two methods are indicated by solid dots. The shaded areas show the amount of deviation of the means from zero which would be expected if there were no relationship between asymmetry and capacity for seed production.

It is unnecessary to represent the relationship between the results of r_{as} and the $F_o - F_e$ method graphically, since the correlation between the partial correlations and the mean deviations is so close that the graph already published for the mean deviation and the $F_o - F_e$ method (HARRIS 1917 a, diagram 3) is, for all practical purposes, identical with it.

RECAPITULATION

In earlier papers it has been shown that there is a negative correlation between bilateral asymmetry in the unilocular fruit of *Phaseolus* and its capacity for maturing its ovules into seeds, asymmetrical fruits being less capable of seed development than symmetrical.

While the two proofs of the existence of the relationship there employed are quite valid, they do not express the intensity of the correlation on the universally comparable scale of -1 to $+1$. This has been the purpose of the present paper.

PEARSON'S bi-serial r has been shown to be a suitable constant for measuring the correlation between asymmetry and actual numbers of ovules and seeds per pod. The influence of the correlation between the number of ovules and the number of seeds per pod upon the correlation between asymmetry and the number of seeds matured has been eliminated by the use of the partial correlation formula for three variables, one of which is constant.

The results are, therefore, expressed in terms of the partial correla-

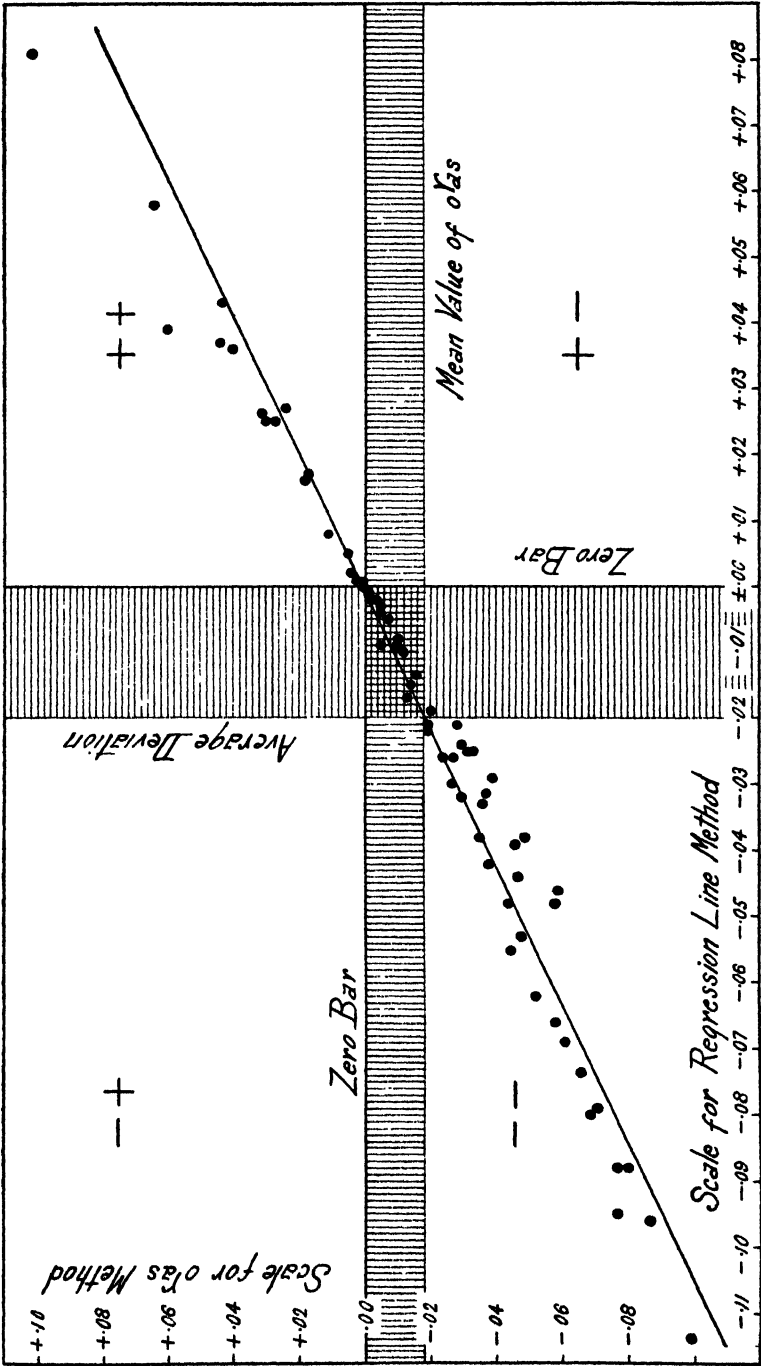


DIAGRAM 1.—Correlation between deviation from regression straight line method and partial correlation method of measuring relationship between asymmetry and capacity for seed production.

tion between asymmetry and number of seeds matured for constant number of ovules per pod.

The constant is found to be of a very low order. The average value of r_{as} for the 69 series of *Phaseolus* now available is about $-.029$.

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QUADRUPLE HYBRIDS IN THE F_1 GENERATION FROM *OENOTHERA NUTANS* AND *OENOTHERA PYCNOCARPA*, WITH THE F_2 GENERATIONS, AND BACK- AND INTER-CROSSES¹

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INTRODUCTION

One of the many interesting and remarkable features of the evening primroses of the genus *Oenothera* (section *Onagra*), is the large number of distinct genetic types in the species *Oenothera "biennis"*, as generally understood in North America. In many localities a superficial examination will reveal distinct types in the population of this "species".

¹ An account of three of the hybrids was presented before the American Phil. Soc. at its general meeting in April, 1914 (see ATKINSON 1914). This paper was accepted by the *Zeitschr. f. ind. Abst. u. Vererb.*, and the proof was read in October, 1914, but the European war has probably prevented its publication. An account of the F_2 generations, and back- and inter-crosses, was presented at the general meeting of the Am. Phil. Soc. in April 1916. Only very brief abstracts of any portion of this work have as yet been published.

These types differ either in the character of the flowers, stems, foliage or rosettes, or in all combined. Certain types manifest great resistance to the attacks of certain fungi, especially to *Peronospora*. The juices of certain types are preferred by the tarnished plant bug. The seeds in some forms present striking differential characters.

In the vicinity of Ithaca, N. Y., as the result of a partial survey of a very small portion of territory, I have found a dozen different forms in the so-called "*biennis* alliance", which in cultivation have proven to be distinct types. The uniformity of character shown in the rosettes, as well as in the mature plants, in the population bred from each of these types, is remarkable, and dispelled the suspicion at first entertained that the different forms recognizable in the field might be merely fluctuating modifications in a very "variable" species. Some of them differ by so many characters and manifest such strikingly different genetic constitutions, that they evidently represent different specific types. Sev-



FIG. 1

FIG. 2

FIGURE 1.—*Oenothera nutans* Atkinson and Bartlett.

FIGURE 2.—The blend hybrid, *hybrida nutella* (n × p).

eral such distinct specific types have been isolated from the *Oenothera* "biennis" population in the vicinity of Ithaca. BARTLETT (1911, 1913) has isolated a number from several different localities in the United States, and DE VRIES (1913) had previously observed and gathered similar distinct types in this country.

This composite constitution of the "biennis alliance" in North America is reflected in the different concepts of this species in some of the manuals on North American botany, thus rendering it quite impossible, in some localities at least, to correlate any of the forms with the descriptions of *Oenothera biennis* in the manuals. The situation is further complicated by the fact that the true *Oenothera biennis* is probably that referred to by LINNAEUS from the sand dunes of Holland (see BARTLETT 1913, p. 48), where it is believed to be an immigrant from North America, though so far as I know the Holland type of *biennis* has never been observed in our country.

Besides the great number of morphologically different species and varieties in the "biennis alliance" in North America, with their characteristic genetic constitutions, there exists another remarkable peculiarity, noted also in other species of the genus, viz., the marked power which some of these types have to produce splitting in the F_1 progeny of certain crosses, while others lack it, or possess it only to a very limited degree. DE VRIES (1913) has clearly demonstrated this variability in splitting power of certain species of *Oenothera*.

During the summer of 1909, on a small area of an abandoned pasture, which I was developing as a private wild garden, just within the limits of the city of Ithaca, there were a number of self-sown evening primroses. No critical examination was made of them, but as I passed among them almost daily I finally became aware, perhaps by a process of unconscious differentiation, that certain individuals had red stems and red mid-veins of the leaves, while other individuals had green stems and white mid-veins. These were the only differential characters which attracted my attention that season, as I was not aware at that time of the fact that *Oenothera* "biennis" was a composite species embracing a large number of elements which breed as distinct species and forms. It occurred to me that it might be interesting to hybridize these forms for the purpose of observing the distribution of color in the hybrids and in their progeny. Cross pollinations were then made between two selected individuals, one of each type. But seed was obtained that year only from the green-stemmed individual fertilized by the use of pollen from the red-stemmed one.

Being absent from Ithaca during the summer of 1910, the seed was not sown until the spring of 1911. Seed from each parent, saved from protected flowers, was also sown. The young seedlings were transplanted from the seed pans to flats in the usual way and when of suitable size they were transplanted to the garden. They were not forced by planting early, and were therefore grown as biennials. During mid-summer marked differences began to appear in the rosette leaves, which became very striking during the autumn. The rosette leaves of the parents differed by five or six characters, and it was evident that there were at least two hybrid types. The hybrid types, however, could not be very well determined because many of the rosettes were more or less severely attacked by the downy mildew (*Peronospora Arthuri*), while many of those of the green-stemmed parent were more severely injured.

The following season (1912) the plants came into flower. A critical study revealed further striking differences between the two parents. The differential characters relate to habit, leaves, stems, inflorescence, flowers, and seed pods, altogether some 25-30 characters being noted by which the two forms differed. The two forms were very distinct from *Oenothera biennis* as recognized by DeVRIES, BARTLETT and others, and were regarded as undescribed species. They were submitted to BARTLETT who confirmed this opinion and they were described as *Oenothera nutans* Atkinson & Bartlett, and *Oe. pycnocarpa* Atkinson & Bartlett. For a complete diagnosis of the two species the original descriptions (see BARTLETT 1913, p. 81) should be consulted, but a brief synopsis of the characters is given below.

All of the cultures were carried out in fairly rich garden soil and some tillage was given, enough to keep down weeds and to stir the soil several times, particularly during rosette development and during the spring of the second season. Under these conditions the full expression and strength of characters are realized. These characters relate to the habit and coloration of the adults; features of the rosettes, foliage and inflorescence. The habit and morphological characters are well shown in the photographs here reproduced. The measurements given are for the garden cultures.

Oenothera pycnocarpa. *Habit*: tall, 1—1.5 m; lower stem branches numerous, strict, not widely spreading, reaching about the middle of the main stem, main stem therefore with high over-top, tips nearly the same level; axillary rosettes over the middle and upper part of the main stem, or short flowering branches just below the main inflorescence.

Autumnal rosettes compact, the larger leaves (late summer and early autumn leaves) narrow, deeply cut over the basal half, furrowed, repand, white-veined, plain or only slightly buckled, no reddish spots. *Stems* green, (rarely tinged red on a portion of the sunny side), tubercles green. *Stem leaves* drooping, narrow, white-veined, slightly sinuate-toothed (lower leaves strongly so over basal portion), furrowed, plain, no red spots. *Inflorescence* long and dense; bracts green, slightly sinuate-toothed, longer than the flower buds, persistent, basal ones longer than the pods. *Petals* lemon yellow, cuneate, strongly emarginate, not plicate, edge plain, medium size, firm, not quickly wilting. *Fertility* high (pods with many viable seeds). *Plant* flowering for a long period and maturing late. See figures 5, 8 and 13.



FIG. 3



FIG. 4

FIGURE 3.—The selective hybrid, *hybrida pycuella* ($n \times p$).

FIGURE 4.—The selective hybrid, *hybrida tortuosa* ($n \times p$). The main stem is fasciated and has split into two branches, the height or over-top of the main stem is therefore probably not so great as it would have been if it were not for the fasciation.

Oenothera nutans. *Habit*: medium height, .75—1.00 m; lower stem branches numerous, spreading irregularly, reaching far above the middle of the main stem, main stem therefore with low over-top, tips at unequal heights, not terminating at the same level; axillary rosettes over the middle portion of the stem; short flowering branches at base of the main inflorescence. *Autumnal rosettes* compact, the larger leaves broad, sinuate-toothed over the basal portion, convex, not repand, red-veined, strongly crinkled, reddish spots in the autumn. *Stems* dark red, sometimes also the base of the inflorescence axis is red, otherwise the inflorescence axes are green; tubercles red, even over the green parts of the stem, rarely red on the young pods. *Stem leaves* broad, very slightly sinuate-toothed over the basal portion, flat or convex, red-veined, plain or somewhat crinkled, few or no red spots. *Inflorescence* medium length, dense, sometimes lateral; bracts usually pale green and caducous, except sometimes a few of the basal ones are green and persistent, small and shorter than the flower buds, edge plain. *Petals* chrome yellow, obovate, or scarcely emarginate, plicate, edge eroded, weak, soon withering, medium size, but larger than in *Oe. pycnocarpa*. *Fertility* high. *Plant* maturing early (in late summer or early autumn). See figures 1, 8 and 9.

Besides several minor deviations, of little consequence here, there is an important variation which should be taken into account and clearly understood. This variation consists in the production of annual individuals by biennial species. This is particularly liable to happen in artificial cultures, and sometimes is encouraged by the investigator for the express purpose of saving time. Where seeds are sown during the winter and the seedlings have reached some size by the time the growing season permits transplanting to the garden, the influence of the warm summer season on these more advanced seedlings may stimulate them to early stem growth so that they flower and fruit in a single season. In some cases a large percentage, or the total, of the culture may form annuals, while a small percentage, or none, pass on to the rosette form. Where the species contrasted have autumnal rosettes with strikingly different character composition, the annuals, in the case of some species, fall far short of presenting the full complexion of the specific character. This is true of the two species here studied as well as of their hybrids. The annual forms of *pycnocarpa*, produced in culture in 1913, and again in 1914 and 1915 came into flower early except those of one lot from a seven-carpeled pod in 1914. Those grown as annuals formed no mature rosettes. The later leaves of the rosettes, and the lower

stem leaves of these annual forms, were very strongly toothed over the basal portion, but did not approach the cut condition of the later leaves of mature autumnal rosettes.

If cultures are started in March or April, and the seedlings grown in 2-inch pots until they become pot-bound, all or a percentage may develop as true annual forms, depending on the way the cultures are handled. In the cultures of 1914, some individuals of *nutans* came into flower early in July, others in August, and a very few formed only rosettes which were quite well formed early in August, and characteristically mature in September.

Since the rosette leaves developed in late summer and early autumn attain a higher degree of morphological differentiation than the spring and early summer leaves, the complete life cycle and full expression of the species is not obtained when these species are grown as annuals. The annuals of biennial species reach the flowering and fruit period by short-circuiting the complete life history. They are really



FIG. 5

FIG. 6

FIGURE 5.—*Oenothera pycnocarpa* Atkinson and Bartlett.
FIGURE 6.—The blend hybrid, *hybrida nutella* ($p \times n$).

short-circuit forms with paedogenic rosettes. Sometimes in greenhouse cultures seeds falling from ripe pods of a potted plant during the winter, germinate, and under the warm conditions of hothouse culture begin stem development early, omitting the rosette stage. Such short-circuit forms, in species where late summer and early autumn leaves of autumnal rosettes are strongly cut over the basal portion, and the stem leaves are only slightly cut, or toothed, suggest a variation in the leaves due to the influence of the changed environment, and thus may be misleading. The cycle has been shortened from early rosette leaves slightly cut to lower stem leaves slightly cut, omitting the late-formed strongly cut leaves of the mature rosette stage.² All gradations sometimes appear between the extreme short-circuit forms and those with the rosette stage complete, the degree of rosette development reached depending on the time at which stem development begins. So far as I am aware the conditions have not yet been analyzed which determine the time of stem development in these annual forms of biennial species.

THE F₁ HYBRIDS FROM *OENOTHERA NUTANS* AND *OE. PYCNOCARPA*

As already noted, the injury to many of the rosettes in the 1911 cultures of the cross *Oe. pycnocarpa* (green stem) × *Oe. nutans* (red stem), from the attacks of the *Peronospora* prevented a satisfactory analysis of the hybrid types. In the following year (1912) these biennial forms which were not seriously injured by the parasite came into flower. There were two distinct hybrid types. One of these appeared to be a blend, but the petals were more like those of *Oe. nutans*, though larger than those of either parent. It has been named *Oe. hybrida nutella*. It proved to be self-sterile. The other hybrid was selective, receiving certain characters from each parent and developing them to their full expression. The flowers were exactly like those of *Oe. pycnocarpa*, and it has been named *Oe. hybrida pycnella*. It is self-fertile to a very high degree.

Because of the injury to the rosettes parasitized by the *Peronospora*, the experiments were repeated. It was also desirable to study the reciprocal crosses between the two species. Therefore reciprocal cross-pollinations of the parents in the first generation of the garden cultures were made in 1912.

The seed of these reciprocal crosses, as well as of the two parents, was

² Exactly such short-circuit annual forms appeared in an undescribed species, No. 17 of my 1913 cultures, about 50 percent being short-circuit forms, while the remainder which came into flower in 1914 formed mature rosettes with leaves strongly cut over the basal half.

sown in seed pans during March 1913. When the seedlings were furnished with 4 or 5 leaves they were transplanted to flats, and then when of suitable size were transplanted to the garden in May. Some developed as annuals and began to flower in July, while others formed autumnal rosettes and did not flower until the season of 1914. Of the hybrids which came into flower during July and August it was evident that there were two distinct types, and these two types were identical with the two hybrid types obtained the previous year. Furthermore, these two hybrid types appeared on each side of the reciprocal crosses.



FIGURE 7.—The selective hybrid, *hybrida pycnella* ($p \times n$).

In the seedling stage, as well as in the early rosette stage it was quite impossible to differentiate the parents except for occasional red spots in the leaves of the red-stemmed parent, and as the leaves became larger the mid-veins of this parent also began to show the red color. Likewise it was impossible to distinguish the hybrid types, either from each other or from either parent. But when the annuals began stem development it was possible to differentiate the parents and hybrid types from the character of the lower stem leaves, but not with such certainty as at the flowering period or in the well developed autumnal rosettes.

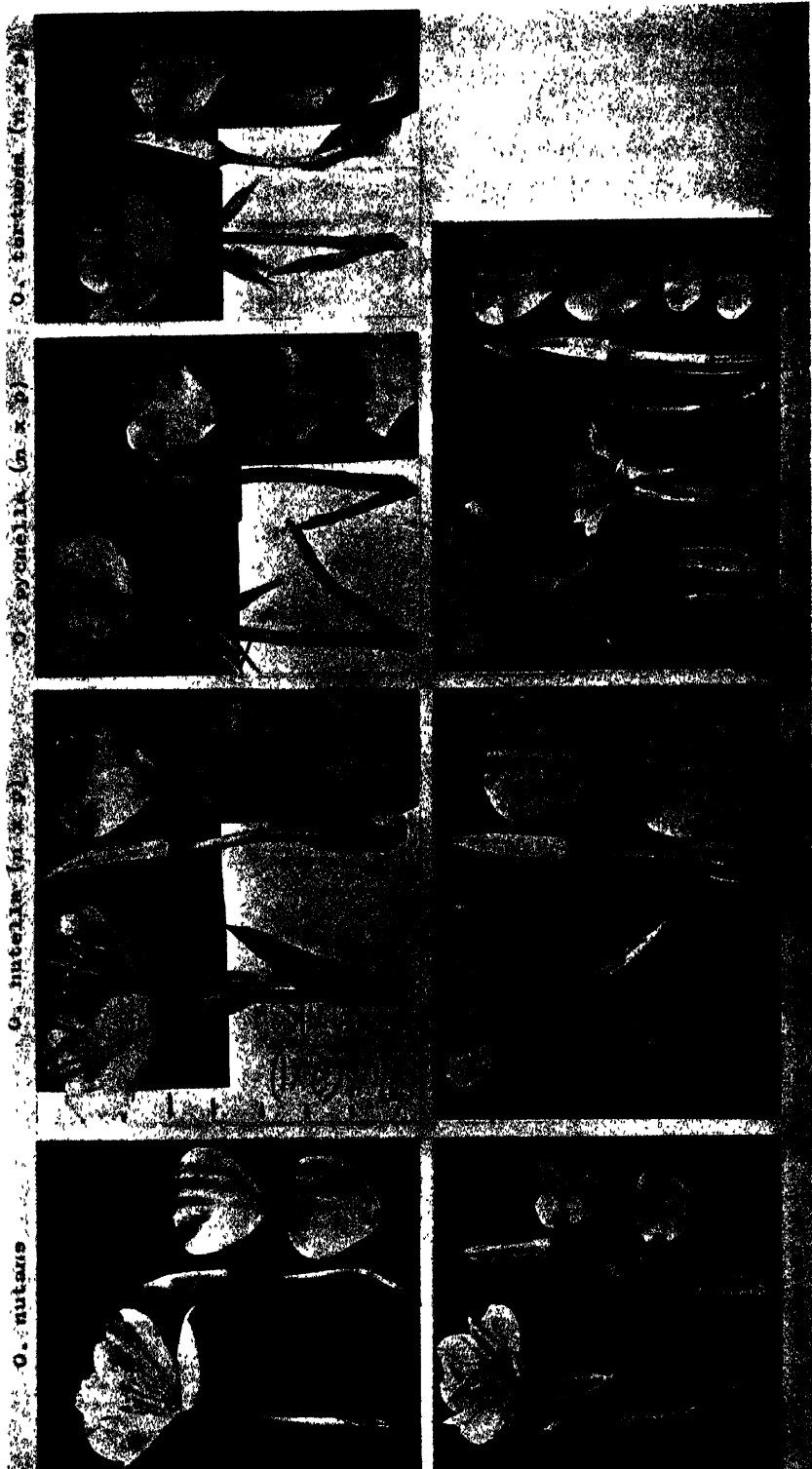


FIGURE 8.—Details of flowers and buds. The upper row contains *Oe. nutans* and three of the hybrid types when *nutans* is the mother. The lower row contains *Oe. pycnocarpa* and the two hybrid types when *pycnocarpa* is the mother. The parents are in the first column; the blend, *hybrida nutella*, in the second column; the selective, *hybrida pycnella*, is in the third column; and *hybrida tortuosa* (also a selective hybrid) is in the upper right-hand corner.

The remaining hybrid rosettes, those which did not proceed to stem development that season, could not be differentiated into types during July or early August. But as they approached the autumnal stage the new and larger leaves began to display the differential characters which permitted sorting into distinct types with a fair degree of accuracy, and when mature in September three distinct hybrid types were easily recognizable, the third type not producing annual forms that season. This third hybrid type is named *hybrida tortuosa*, because the mature autumnal rosette leaves are often more or less strongly twisted due to their narrow, convex, crinkled form. The following season (1914) the biennial individuals, those with the mature autumnal rosettes in 1913, came into flower, and four hybrid types in the F_1 generation of the cross were distinguished.³ The fourth type had the rosette characters of the third but the stem color of the mature plant was green instead of red as in *tortuosa*. It is named *hybrida tortuella*.

*Characters of the four hybrids of the F_1 generation compared
with the parents*

The principal characters of the F_1 hybrids may now be given. For the purpose of easy comparison the principal contrast characters of the parents are repeated.

Oenothera nutans. Rosette leaves broad, with a few rather prominent teeth over the basal part of the blade, convex, crinkled, red-veined; stems red; stem leaves spreading; petals obovate, overlapping, fluted, distal margin eroded and plain, quickly wilting; pods short, usually crowded; plants maturing early, very fertile; progeny very uniform.

Oenothera pycnocarpa. Rosette leaves comparatively narrow, deeply cut over the basal half of the blade, furrowed, repand, plain or somewhat buckled, white-veined; stems green; stem leaves depressed; petals cuneate, not meeting, not fluted, distal margin not eroded, notched, rather firm and wilting late; pods comparatively long, often crowded; plants maturing late, very fertile; progeny very uniform.

Oenothera hybrida nutella. A blend⁴ hybrid. Rosette leaves flat, intermediate in width and edge characters between the two parents, the basal part of the mature autumnal leaves cut about half as deeply as in the *pycnocarpa* parent; stems pink; stem leaves spreading; petals larger than those of either parent, sometimes showing more of the *nutans* char-

³ For the proportional numbers of these hybrid types in the reciprocal crosses see the tables 2 to 9.

acter, more rarely the *pycnocarpa* character dominates; absolutely self-sterile so far as tested, though pollen and egg cells are both functional in crosses with other forms; pods rather long, lax; plants maturing late, flowering for a long period.

Oenothera hybrida pycnella. A selective⁴ hybrid. Rosette leaves broad, with a few rather prominent teeth over the basal part of the blade, furrowed, repand, plain; stem leaves spreading; stems green; flowers exactly like those of *Oc. pycnocarpa*; pods rather long, moderately dense; plants maturing early, very fertile; type fixed in the F_1 generation, breeds true, progeny very uniform.

Oenothera hybrida tortuosa. A selective hybrid. Rosette leaves



FIGURE 9.—Autumnal rosette of *Oenothera nutans*.

⁴ The term "blend" hybrid is here used in the usual acceptance of the term. The allelomorphous factor pairs blend so that a form intermediate between the two appears. The term "selective" hybrid applied to the three other hybrids of the F_1 has reference to the fact that only one factor of each homologous pair is selected for expression in a given hybrid, from those in the F_1 zygote, the other factors being subordinated. The factors selected come from both parents.

comparatively narrow, deeply cut over the basal half of the blade, convex, crinkled, red-veined, often more or less twisted (probably a result of the tension from strong convexity and crinkledness of the narrow leaves); stems red; stem leaves convex, depressed, a few rather strong, distant teeth over base of blade; flowers exactly like those of *nutans*; pods short, dense (or crowded) like those of *nutans*; plants maturing late, very fertile; type fixed in the F_1 generation, breeds true; progeny very uniform.

Oenothera hybrida tortuella. A selective hybrid. This hybrid appears to have all the characters of *hybrida tortuosa* in the first generation, except the red stem, a *nutans* character, *hybrida tortuella* having the green stem of the parent *pyncocarpa*; very fertile; type not fixed in the F_1 generation, since in the F_2 generation it breaks into a number of types



FIGURE 10.—Rosette of blend hybrid *nutella* ($n \times p$). Note the intermediate width and edge character of the leaves.

showing great variations. This fourth hybrid appears in very small numbers compared with the others.⁵

A single individual of *hybrida tortuella* appeared in the 1913-14 cultures. In the autumn of 1913 its rosette was classed as a *tortuosa*. It caused considerable surprise in 1914 when it came into flower that its stem should be green, since I had forecast a red stem for all the plants with *tortuosa* rosettes.

The photographs reproduced here present in graphic form nearly all



FIGURE 11.—Rosette of selective hybrid, *hybrida pycnella* ($n \times p$). Observe the broadness and toothedness of the *nutans* leaves.

⁵ The plants were not grown in large enough numbers to determine whether or not there is any regularity in the ratios of the different hybrid types appearing in the first generation. In the cross *nutans* \times *pycnocarpa* (1913 culture) there were 108 plants in the garden culture. Of these 35 were annual *nutella*, and 10 were annual *pycnella*, 21 *tortuosa* and 1 *tortuella*. Of the reciprocal cross (*pycnocarpa* \times *nutans*) only 51 plants were grown in the garden. Of these 4 were annual *nutella*, 9 were annual *pycnella*. There were 38 which formed autumnal rosettes, 36 *pycnella* and 2 *nutella*.

the characters of the two parents and their four hybrids. The fact that the parents differ by so many strong contrast characters, the majority of which under normal culture are so clear-cut and strikingly different in the two parents, permits a very satisfactory study of the transmission of the characters, and their composition in the F_1 hybrids.

The habit of the plants is shown in figs. 1 to 7, all from biennials. Figure 1 represents *nutans*, and figures 2 to 4 show three of the hybrid types of the cross *nutans* \times *pycnocarpa*; figure 2 is the F_1 blend hybrid,



FIGURE 12.—Rosette of selective hybrid, *hybrida tortuosa* ($n \times p$). Note the narrowness and cutness of *pycnocarpa* and the crinkledness and convexity of *nutans* in the leaves.

nutella; figure 3 the green-stemmed F_1 selective hybrid, *pycnella*, and figure 4 the red-stemmed F_1 selective hybrid, *tortuosa*.

In figure 8 are presented details of the inflorescence.⁶ The differences

⁶ It was rather late in the season when the flowers of *nutans* and *pycnella* ($p \times n$) were photographed, and the bracts were not quite so large as the earlier ones.

in the petal characters are striking. The upper row contains *nutans* at the left, and then follow in order three of the hybrid types (*nutella*, *pycnella* and *tortuosa*) when *nutans* is the mother. The lower row contains *pycnocarpa* at the left, and two of the hybrid types (*nutella* and *pycnella*) when *pycnocarpa* is the mother. *Tortuella* is not shown, its



FIGURE 13.—Rosette of *Oenothera pycnocarpa*.

flowers being like those of *tortuosa*. The petals of *tortuosa* are clearly those of *nutans*, and the petals of *pycnella* are clearly those of *pycnocarpa*. The petals of *nutella* are often very like those of *nutans*, particularly as regards the plaited character and oboval form. They are, however, larger than those of *nutans*. The emargination is more pronounced, showing more of the *pycnocarpa* character. Sometimes the plaited character is not so pronounced, as is evident in the photograph of *nutella* ($n \times p$). But in many examples the plaited character is very evident. While, therefore, the petals of this blend hybrid (*nutella*) more strongly resemble those of *nutans*, they are modified by those of *pycnocarpa*, the blend in the petal characters being less striking than in the vegetative characters.

The rosettes of *nutans* \times *pyncocarpa* are reproduced in figures 9 to 12; those of *pyncocarpa* \times *nutans* in figures 13 to 15. Figure 9 is the mother *nutans*; figure 10 is the F_1 blend, *hybrida nutella*. The *hybrida nutella* rosette of the reciprocal cross (*pyncocarpa* \times *nutans*) is shown in figure 14. By a comparison with the rosettes of the parents (for the



FIGURE 14.—Rosette of the blend hybrid, *hybrida nutella*, from the cross *pyncocarpa* \times *nutans*.

rosette of *Oe. pyncocarpa* see figure 13), the blending of the characters, wideness with narrowness, and cutness with toothedness, is very evident.

In figure 11 is shown a rosette of the F_1 selective, *hybrida pyncella*, from the progeny when *nutans* was the mother, and in figure 15 the same form when *pyncocarpa* was the mother. The two have the same composition of characters, but *pyncella* ($p \times n$) has fewer leaves, selected because the leaf detail could be better represented in the photograph. The photograph shows the selection of the width and toothed character from *nutans*. Furrowedness and repandness come from *pyncocarpa*, but are

not shown well in the photograph. At the time the photographs were made furrowedness had not been recognized as a character and considerable effort was made to flatten the leaves down so that the edge characters would appear to better advantage.

In figure 12 is the F_1 selective *hybrida tortuosa*. This is as yet represented only from the progeny when *nutans* is the mother. It has not yet appeared in the cultures of *pycnocarpa* \times *nutans*. This is quite a remarkable rosette. The larger leaves have the narrowness and cutness of *pycnocarpa*, the crinkledness and convexity of *nutans*, all these characters being clearly represented in the photograph. It has also the red-veinedness of *nutans*.



FIGURE 15.—Rosette of selective hybrid, *hybrida pycnella*, from the cross *pycnocarpa* \times *nutans*.

In diagram 1 the principal characters which have been studied, are tabulated in such a way as to show the blending of the contrast characters of the two parents in the F_1 *hybrida nutella*, and also the sorting of

characters from the two parents with their recombination into new complexes, or mosaics,[†] in the F_1 selectives, *hybrida pycnella* and *hybrida tortuosa*. In the upper line are arranged the characters of *nutans*, in the lower line those of *pycnocarpa*, while in the middle line are arranged those of *hybrida tortuosa*, *hybrida nutella* and *hybrida pycnella*. The lines indicate the source and distribution of characters.

The abbreviations in the diagram are explained in table 1. *Hybrida tortuella* had not been detected when this diagram was made. But its phenotype in the F_1 is so like that of *hybrida tortuosa* (but having a green stem instead of the red stem of *tortuosa*) it is better to not complicate the diagram by its introduction.

As seen by an examination of diagram 1 there is a distinct linking or association, of certain factors in their transmission to the F_1 selective hybrids, *pycnella* and *tortuosa*. There is a splitting of the total factor composition of certain members of the plant body. The splitting, however, occurs almost entirely *between* factors, not *through* them, so that certain factors, or groups of factors, are transmitted entire to one or the other of the F_1 selective hybrids. Examples of this linking or association of characters are as follows: First, color characters; second, petal characters; third, broadness and toothedness of rosette leaves; fourth, narrowness and cutness of rosette leaves; fifth, crinkledness, convexity and red-veinedness of rosette leaves; sixth, plainness, furrowedness and white-veinedness of rosette leaves (in *hybrida pycnella* the mid-veins of the leaves are often tinged with red). The linked characters are inherited as follows by the two F_1 selectives, *pycnella* and *tortuosa*:

In *hybrida pycnella* the habit is taken from *nutans*; the rosettes take the broadness and toothedness of the leaves from *nutans*; the furrowedness, repandness and plainness of the leaves come from *pycnocarpa*; the green stem and green tubercles come from *pycnocarpa*; width and edge character of stem leaves come from *nutans*; the size and persistency of the bracts are derived from *pycnocarpa*; all the petal characters come from *pycnocarpa*. It will be noted that the green stem and petal characters come from *pycnocarpa*, but it may not be a case of linking between petal characters and stem color, other than that of their association in the parent *pycnocarpa*.

In *hybrida tortuosa* the habit comes from *pycnocarpa*; the rosette leaves take the narrowness and cutness from *pycnocarpa*; the convexity, crinkledness and red-veinedness from *nutans*; the red stem and red tubercles from *nutans*; width of the stem leaves comes from *nutans*, but

[†] These mosaics are of a different kind from those described by BLARINGHEM (1913).

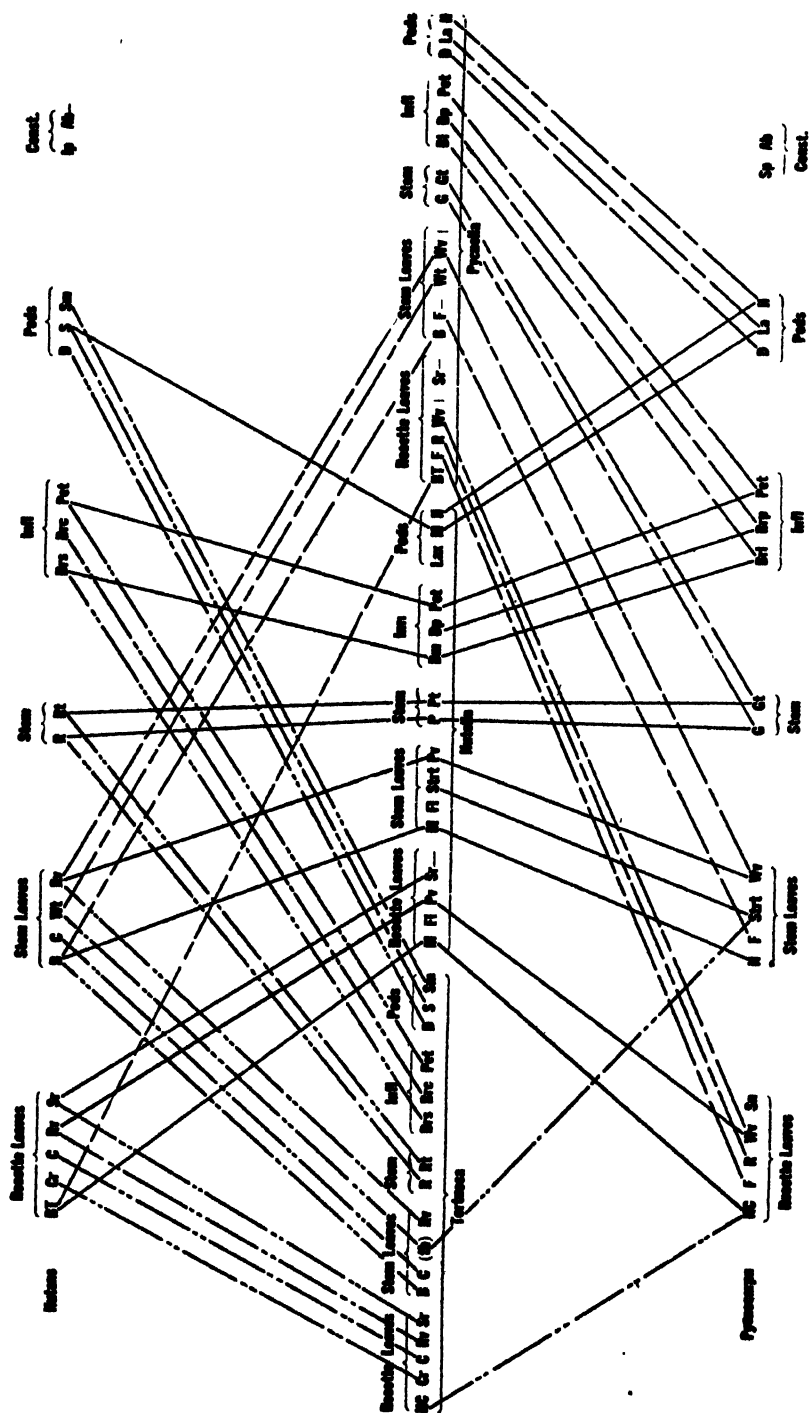


TABLE I

Key to the abbreviations used in diagram I

	<i>Nisians</i>	<i>Tortuosa</i>	<i>Nisiella</i>	<i>Pycnella</i>	<i>Pycnocarpa</i>
Rosette leaves	$\left\{ \begin{array}{l} \text{BT} = \text{broad and toothed} \\ \text{Cr} = \text{crinkled} \\ \text{C} = \text{convex} \\ \text{Rv} = \text{red-veined} \\ \text{Sr} = \text{spots red} \end{array} \right.$	$\left\{ \begin{array}{l} \text{NC} = \text{narrow and cut} \\ \text{Cr} = \text{crinkled} \\ \text{C} = \text{convex} \\ \text{Rv} = \text{red-veined} \\ \text{Sr} = \text{spots red} \end{array} \right.$	$\left\{ \begin{array}{l} \text{M} = \text{medium broad} \\ \text{Fl} = \text{flat} \\ \text{Pv} = \text{pink-veined} \\ \text{Sr} = \text{some red spots} \end{array} \right.$	$\left\{ \begin{array}{l} \text{BT} = \text{broad and toothed} \\ \text{F} = \text{furrowed} \\ \text{R} = \text{repand} \\ \text{Wv}^* = \text{white-veined or pink-veined} \\ \text{Sr} = \text{sometimes red spots} \end{array} \right.$	$\left\{ \begin{array}{l} \text{NC} = \text{narrow and cut} \\ \text{F} = \text{furrowed} \\ \text{R} = \text{repand} \\ \text{Wv} = \text{white-veined} \\ \text{Sn} = \text{spots none} \end{array} \right.$
Stem leaves	$\left\{ \begin{array}{l} \text{B} = \text{broad} \\ \text{C} = \text{convex} \\ \text{Wt} = \text{weakly toothed} \\ \text{Rv} = \text{red-veined} \end{array} \right.$	$\left\{ \begin{array}{l} \text{B} = \text{broad} \\ \text{C} = \text{convex} \\ \text{(tb)} = \text{strongly and distantly toothed over base} \\ \text{Rv} = \text{red-veined} \end{array} \right.$	$\left\{ \begin{array}{l} \text{M} = \text{medium broad} \\ \text{Fl} = \text{flat} \\ \text{Sirt} = \text{strongly toothed} \\ \text{Pv} = \text{pink-veined} \end{array} \right.$	$\left\{ \begin{array}{l} \text{L} = \text{broad} \\ \text{F} = \text{furrowed, but not usually strongly so} \\ \text{Wt} = \text{weakly toothed} \\ \text{Wv}^* = \text{white-veined or pink} \end{array} \right.$	$\left\{ \begin{array}{l} \text{N} = \text{narrow} \\ \text{F} = \text{furrowed} \\ \text{Sirt} = \text{strongly toothed} \\ \text{Wv} = \text{white-veined} \end{array} \right.$
Stem	$\left\{ \begin{array}{l} \text{R} = \text{red} \\ \text{Rt} = \text{red tubercles} \end{array} \right.$	$\left\{ \begin{array}{l} \text{R} = \text{red} \\ \text{Rt} = \text{red tubercles} \end{array} \right.$	$\left\{ \begin{array}{l} \text{P} = \text{pink} \\ \text{Pt} = \text{pink tubercles} \end{array} \right.$	$\left\{ \begin{array}{l} \text{G} = \text{green} \\ \text{Gt} = \text{green tubercles} \end{array} \right.$	$\left\{ \begin{array}{l} \text{G} = \text{green} \\ \text{Gt} = \text{green tubercles} \end{array} \right.$
Inflorescence	$\left\{ \begin{array}{l} \text{Brs} = \text{bracts small} \\ \text{Brc} = \text{bracts caducous} \\ \text{Pet} = \text{petal characters} \end{array} \right.$	$\left\{ \begin{array}{l} \text{Brs} = \text{bracts small} \\ \text{Brc} = \text{bracts caducous} \\ \text{Pet} = \text{petal characters} \end{array} \right.$	$\left\{ \begin{array}{l} \text{Bm} = \text{bracts medium} \\ \text{Bp} = \text{bracts persistent} \\ \text{Pet} = \text{petal characters} \end{array} \right.$	$\left\{ \begin{array}{l} \text{Bl} = \text{bracts large} \\ \text{Bp} = \text{bracts persistent} \\ \text{Pet} = \text{petal characters} \end{array} \right.$	$\left\{ \begin{array}{l} \text{Brl} = \text{bracts large} \\ \text{Brp} = \text{bracts persistent} \\ \text{Pet} = \text{petal characters} \end{array} \right.$
Pods	$\left\{ \begin{array}{l} \text{D} = \text{dense} \\ \text{S} = \text{small} \\ \text{Sm} = \text{smooth} \end{array} \right.$	$\left\{ \begin{array}{l} \text{D} = \text{dense} \\ \text{S} = \text{small} \\ \text{Sm} = \text{smooth} \end{array} \right.$	$\left\{ \begin{array}{l} \text{Lax} = \text{lax} \\ \text{M} = \text{medium size} \\ \text{H} = \text{hairy} \end{array} \right.$	$\left\{ \begin{array}{l} \text{D} = \text{fairly dense} \\ \text{La} = \text{large} \\ \text{H} = \text{hairy} \end{array} \right.$	$\left\{ \begin{array}{l} \text{D} = \text{dense} \\ \text{La} = \text{large} \\ \text{H} = \text{hairy} \end{array} \right.$
Constitution	$\left\{ \begin{array}{l} \text{Ip} = \text{immune to Peronospora} \\ \text{Ab} = \text{attacked by bugs slightly} \end{array} \right.$				$\left\{ \begin{array}{l} \text{Sp} = \text{susceptible to Peronospora} \\ \text{Ab}+ = \text{attacked by bugs} \end{array} \right.$

the edge character is different from either parent; the size and caducous character of the bracts are derived from *nutans*; all the petal characters come from *nutans*. In the mature state, when rosette leaves are not present, *tortuosa* resembles *nutans* very strongly, the habit, drooping of the leaves, and edge character of the stem leaves being the only differential characters in this stage. There are a few rather prominent and distant teeth on the base of the blade,⁸ a very different character from the rather regularly serrate leaves over the middle and upper part of the stem of *pycnocarpa*, and the nearly plain edge of the stem leaves of *nutans*.

In *hybrida tortuella* the phenotypic characters of the F_1 are derived as in *tortuosa*, but instead of receiving the red stem of *nutans*, it takes the green stem of *pycnocarpa*. There is here a crossing over of stem color and flower character as compared with the two other selective hybrids.

While all the contrast vegetative characters possessed by the two parents are transmitted, each in its entirety, to the two F_1 selectives, some to *pycnella*, the others to *tortuosa*, the F_1 blend, *hybrida nutella*, inherits all, or a very large proportion of the contrast characters of the two parents. In such a case it is impossible for both characters of the "allelomorphic pair" to express themselves in their completeness. Each is modified by the other member of the pair so that an intermediate state between the two contrast characters is attained. The "allelomorphs" blend. In the rosettes, the broadness and toothedness of *nutans* blend with the narrowness and cutness of *pycnocarpa*; the convexity and crinkledness of *nutans* blend with the furrowedness of *pycnocarpa* and the leaves are flat or nearly so. There are no real intergrading forms between the three hybrids, though each one shows slight fluctuations. The red color of the stems and tubercles of *nutans* blend with the green of *pycnocarpa* and an intermediate state of coloration (pink) results. The small bracts of *nutans* blend with the large ones of *pycnocarpa* and bracts of an intermediate size appear on *nutella*.

The F_1 blend hybrid (*nutella*) presents a very interesting case of sterility. When the inflorescence is covered with paper bags, or other screen, to prevent insects from bringing foreign pollen to the stigma, no seeds are developed. Though the pods often attain a considerable size and give the impression that seed is being formed, they are found to be

⁸ The few rather prominent teeth over the base of the stem leaves recalls the same feature of the lower stem leaves of the parent *pycnocarpa*, but the stem leaves of *tortuosa* with this character have a more extensive distribution on the stem than is the case in *pycnocarpa*.

hollow, and finally die. This is not due to a failure in pollination, for, like the parents, and others of the smaller-flowered *oenotheras*, pollination takes place in the bud. In the summer of 1912, when it was discovered that protected flowers were not setting seed, a large number were hand-pollinated. Not only was pollen from the same flower used in some cases, and in others pollen from different flowers of the same individual, but cross-pollinations between different individuals were also made. No seed formed. During the summer of 1913 a much larger number of hand-pollinations were made. Several inflorescences were also protected by covering with paper bags. In no case did seed develop. A large number of hand-pollinations were again made in 1914, using not only *nutella* ($n \times p$) but *nutella* ($p \times n$) in reciprocal cross-pollinations. No seed was formed. The same results were obtained in 1916.

The sterility of the blend hybrid (*nutella*) is not due to sterility of the pollen or egg cells. Flowers which are unprotected, if visited by bees which have access to the parents or other species, growing in proximity, set an abundance of viable seed. When hand-pollinated, using pollen from either parent, from *hybrida pycnella*, *hybrida tortuosa*, from *Oe. grandiflora*, *Oe. Lamarckiana*, and some other species, an abundance of viable seed is formed. The pollen is well formed, showing a small, and no greater, percentage of poor grains than either of the parents. It is effective when placed on the stigma of either parent, on *hybrida pycnella* and *hybrida tortuosa*, on *Oe. grandiflora*, *Oe. Lamarckiana*, and other species.

The cause of the sterility of *hybrida nutella*, therefore, has not been determined. But it may be due to a lack of correlation in certain of the physiological processes among the blended "factors," or characters, inherited from the two parents. Or it may be due to a lack of blending among some of the homologous characters, structures or physiological processes or parts of the inflorescence. If a complete and equal blending of all homologous factors for the inflorescence took place, it may be that the reproductive processes would present as high a degree of efficiency as the vegetative processes have. That the phenomenon of blending of all the homologous factors for the inflorescence does not take place is shown by the petals, which are far more like those of *nutans* than of *pycnocarpa*. The blending of certain parental characters in the inflorescence, the taking over of others in their entirety from one parent with the exclusion of their homologues, and possibly the incomplete blending or unequal sharing in the union of others may produce an organization ineffective for the reproductive processes. Certain of the "qualities" or

properties combined in the egg, or pollen, or both, may lack the reciprocal influences necessary to a union of sperm and egg, although sperm and egg are effective in other combinations. It is also possible that certain physiological properties may retard the growth of the pollen tube when the flowers are selfed, but may not be effective against the growth of the tube from foreign pollen. Some preliminary studies indicate that the pollen tube does not grow rapidly enough down the style to reach the egg in time.

Whatever may be the nature of the lack of a reciprocal working of the reproductive mechanism in *hybrida nutella* it can not be attributed to irregularities in the meiotic division preceding the formation of the pollen, such as have been shown by JUEL (1900, p. 639-641) to take place in *Syringa Rothomagensis* (a hybrid of *S. vulgaris* and *S. Persica*, according to FOCKE 1881, p. 255), where typical mitotic figures are rare in the first division of the gonotokonts. In the atypical cases a process intermediate between mitosis and constriction occurs, a number of chromosomes appear to go to the daughter nuclei undivided, some are left in the cytoplasm. He suggests that there is a lack of mixing of the nuclear substance. Irregularities have also been shown by ROSENBERG (1903, 1904, 1909) in a hybrid between *Drosera rotundifolia* and *D. longifolia*, where there is a difference in the number of chromosomes in the two parents; by CANNON (1903, p. 133) in a *Gossypium* hybrid (*G. Barbadosense* \times *herbaceum*), where some pollen mother cells divide normally, others abnormally; and by METCALF (1901, p. 109) in *Gladiolus* hybrids, where two spindles were observed, presumably due to a repulsion between the paternal and maternal chromosomes, so that they remain in separate groups. These and similar abnormalities in meiotic division may explain the sterility of pollen in certain hybrids. STRASBURGER (1904, p. 609) makes the interesting suggestion that the difficulties resulting in the formation of imperfect pollen occur in synapsis of the heterotypic division.

But, as stated above, this can not account for the sterility of *hybrida nutella*, unless during synapsis (or other critical moments in the formation of the gones) there is an association of physiological "properties" or "tendencies" in the pollen and embryo sac of such a nature as to prevent the reciprocal working of the sperm and egg of *hybrida nutella* when brought together, but permits reciprocal working when either sperm or egg mates with a germ cell of related forms.

The F_1 hybrids of *Nicotiana Forgetiana* crossed with *N. alata grandiflora* are individually self-sterile according to EAST (1915, p. 80) as are

the F_2 , F_3 and F_4 generations. But cross-fertility is high between different individuals of each generation, or between individuals of different generations. The rate of growth of the pollen tubes down the style is so slow that they do not reach the ovary before the flower wilts, when individual plants are selfed. But in cross-pollinations between different individuals of any generation, the growth of the pollen tube is accelerated and reaches the ovary in time to carry the sperm cell to the egg. The self-sterility of individuals is explained by EAST on the ground that the protoplasts of the sex members are alike; and the pollen therefore lacks the kind of enzymes needed to call forth the secretion of a hexose sugar in the style which gives the direct stimulus to the pollen tube in those cases where its growth is accelerated.

The blend hybrid, *Oe. hybrida nutella*, is thus a striking instance of an intermediate hybrid which is totally self-sterile so far as determined. Not only are individual plants sterile, but all members of the race, whatever their origin (i.e. from either side of the reciprocal crosses of the parents), show cross-sterility when bred *inter se*.⁹ But this sterility is not due to an impairment of the fertile condition of either the pollen or egg cells. The self-sterility may be due to a too great likeness of the protoplasm of the sex members as EAST suggests for the individual self-sterility of the *Nicotiana* hybrids. The rate of growth of the pollen tube in *nutella* has not been definitely determined. Some preliminary studies suggest that it grows too slowly to reach the ovules in time.

It does not seem clear how the protoplasm of the sex members of *hybrida nutella* could be any nearer alike than those of each of the parents since the parents are very likely what DeVRIES calls isogamous species. Furthermore the parents, like most small-flowered oenotheras, have a very long historical background of close inbreeding, which according to EAST's suggestions should result in protoplasmic identity in the sexual members. Close and long-continued inbreeding in plants at least, does not in all cases lead to complete sterility resulting in an incompatibility between the germ cells, though it may largely account for partial sterility of the pollen. The somatic cells carry all the factors of the two germ cells, but at the time of the development of the reproductive structures there is a differentiation into maleness and femaleness, manifest in many cases by differentiation in form. Probably also physi-

⁹ In 1916 I had in culture a new race of *nutella* from a cross between *Oe. nutans* of the third generation and a feral individual of *Oe. pycnocarpa*. Cross-pollinations were made between this race of *nutella* and that from crosses between the 3rd generation of the original parents. No seed was formed.

ological differentiation takes place resulting in the formation of different enzymes, etc. The mere fact then, of the coming together of the protoplasm of *nutans* and *pycnocarpa* into the blend *hybrida nutella* would not make the protoplasm of its sex members any more alike than is the case in either of its parents. But the lack of complete blending in certain features of the inflorescence and flowers may prevent certain physiological differentiations necessary to establish a state of compatibility sufficient to permit the coming together and union of the germ cells.

There is another feature which should be considered. The pollen and egg cells may be overloaded with active factors since the sperm and egg cell each carry all or nearly all the factors of both parents of the cross in an active state. If there is physiological incompatibility between sperm and egg, as I am inclined to believe, can it be that this overload of factors, all tending to express themselves as they do in this blend hybrid, has anything to do with this incompatibility?

Correlation between hybrid constitution and relative state of sterility or fertility

The three hybrids present an interesting correlation between their hybrid constitution and their relative state of sterility or fertility. *Hybrida nutella* inherits all the factors of its parents. All the factors are active and only a mean between the homologous characters results. The vegetative characters are a blend. Certain flower structures are combined in such a way as to produce an inefficient reproductive machine and sterility results, although both pollen and egg cell are efficient in other combinations. In *hybrida pycnella* on the other hand, while "inheriting" in its egg cell all of the same factors, there is selected an effective combination of active factors which do not blend. It reaches a very high state of efficiency in its reproductive structures for it possesses a very high degree of fertility. The same can be said of *hybrida tortuosa* in which different factors are selected from the same "inheritance" in its egg cells,—factors which are complementary to those present in *hybrida pycnella*.

Another feature in which the annual forms of *pycnella* differ from either parent is the less dense inflorescence. Consequently the pods are not so crowded as they are in either parent grown as biennials, though the pods are large and crowded with seeds. So far as the parents are concerned, the biennial forms are stocky, and there is a great tendency to fasciation in the stocky individuals on rich soils, much more so in *pycnocarpa* than in *nutans*. No fasciation has been as yet observed in

pycnella, whether annual or biennial forms. While the petals of *pycnella* are usually of the same size as those of *pycnocarpa*, and smaller than those of *nutans*, under certain conditions, not yet determined, they are larger even than those of *nutans*, in size sometimes approaching those of *nutella*.

In the F_1 blend hybrid, *hybrida nutella*, besides the sterility resulting from the lack of correlation in some part of the reproductive machinery, there are some striking modifications in the inflorescence. As already stated, the petals are larger than those of *nutans*, which in turn has larger petals than *pycnocarpa*. The flower buds also average longer, and the spread of the flower is greater.¹⁰ The cause of this progression in the size of the flower has not been determined. It is not accompanied by increased size of other members of the plant body. Possibly it may bear some correlation to the self-sterility, since certain forms of sterility in plants are sometimes accompanied by more showy flowers. It is known also that some hybrids are larger than either parent, but the increase in size here relates only to parts of the flower. The stigma does not over-top the stamens as in many of the large-flowered open-pollinated oenotheras.

Another striking modification in *hybrida nutella* is the lax inflorescence and the consequent lax relation of the pods. This is a characteristic of the annual as well as of the biennial forms.

While *hybrida pycnella* matures early, the annual forms very early, *hybrida nutella* matures late. The annual forms of *nutella*, even though they flower early in some seasons, usually continue to flower until killed by frost in November. It would seem therefore that the earliness of *nutans* is not only inherited by *pycnella*, but also that a progression in this quality has taken place so that the earliness of maturity is intensified. On the other hand, the lateness of *pycnocarpa* is inherited by *nutella* and there appears to have occurred a progression of the quality of lateness in this hybrid.

In *hybrida tortuosa* the edge character of the stem leaves is peculiar, the basal half having fewer teeth than either parent, over the same extent. *Tortuosa* is the only one of the hybrids thus far which may be fasciated, all of the biennial individuals, except one, presenting this character in a marked degree, so that the over-top of the main stem is

¹⁰ In *Oe. pycnocarpa* the spread of the open flower is 20-35 mm, the petals average about 15×15 mm. In *Oe. nutans* the spread of the open flower is 35-42 mm; the petals are 18-32 mm long \times 15-20 mm broad. In *Oe. hybrida nutella* the spread of the open flower is 50-55 mm; the petals are 20-25 mm \times 20-22 mm broad.

not what it otherwise would be. *Tortuosa* also continues to flower longer than *nutans*, this character as well as that of fasciation probably being drawn from *pycnocarpa*.

Difference in habit between annual and biennial forms

The habit of the annual forms of the two hybrids, *pycnella* and *nutella*, is shown by my cultures thus far to be quite different. The plants are lower in stature, and this is true of annual forms of *pycnocarpa* and *nutans*. The lower branches are more spreading, especially those arising in the axils of the rosette leaves, but to some extent also, the lower stem branches. The wider-spreading branches with the lower stature gives to the plant quite a different habit from that of the biennial forms. This variation in form must be taken into account in any comparison of the hybrids with their parents. The habit varies also according to the time in the season at which stem development begins. The earlier in the season stem formation and branching begin, the more nearly normal will the habit be, according to my observations. If stem development is postponed until August or September the lower branches diverge at a wider angle, and often grow for some distance nearly or quite parallel with the surface of the ground, the free end usually curved more or less strongly upward. Many of these branches may be as long or longer than the central axis, but the upward curving tip may not reach the same height as the main stem. This peculiarity has been observed in *hybrida pycnella*, *hybrida nutella* and the cultures of *pycnocarpa*.

Among the 1913 cultures of *pycnocarpa*, where seeds were sown in the greenhouse during March, and the seedlings later transplanted to the garden, in one lot from a seven-carpeled pod only 2 out of 120 plants formed stems and flowers during the first season. Stem development began late in the season, toward the middle or last of August. In one plant the main stem was inclined at an angle of about 45° , and the branches arising from the base of the stem were wide-spreading. In the other plant the main stem grew parallel with the ground and was so rigid that it could not have been brought to the erect position without breaking.

In another race of *Oenothera* from Ithaca, No. 17 of my cultures, a large percentage of annual forms occurred in transplanted seedlings in 1913. Some of these began stem development early enough to mature seed. The branching of these forms was near the normal. But those which began stem development from about the middle of August presented a wide departure from the normal, due to growth of the lower

branches nearly or quite parallel with the surface of the ground, and at a distance from the main axis of 3-5 dm then curved upward. In another species from Ithaca, *Oenothera angustissima* GATES (1913), in my cultures of 1913 a very small percentage began stem development. Two plants came into flower in September. The branches were somewhat more wide-spreading than in the normal forms. Two others began stem development in September forming three or four stems each. None of these stems grew erect. All were prostrate and applied closely to the ground. During the latter part of September and October a dense rosette was formed at the tip of each of these prostrate branches, but no roots had formed. The plants with a large central rosette, and several smaller ones on prostrate stems 2-3 dm from the central rosette presented a very peculiar appearance. This same phenomenon has been observed in other species where stem development begins late.

These variations are epigenetic. They indicate a wide range in the morphological complex, among the individuals of certain species, races or hybrids. The amplitude of this variation is linear, i.e., it extends along the line of the life cycle which becomes short or long, simple or complex, according to epigenetic conditions. But the lateral variations or fluctuations do not meet nor transgress the limits between the species, races or hybrids.

What all of the conditions are which influence this variation in the length of the life cycle, and the lesser or greater degree in the full expression of the maximum characteristics, is difficult to determine. For example, it is difficult to judge the stimulus which determines the beginning of the stem development in the annual forms, which in some cases may occur at almost any time during the season. But when stem development begins, it appears to serve as a stimulus which checks the further development of the rosette, so that the rosettes are arrested in development at different periods. Soil conditions such as fertility, moisture content, etc., probably play a part. The formation of wide-spreading branches, particularly branches which grow for a considerable distance nearly parallel with, or on the surface of the ground, appears to bear some relation to temperature, especially to the seasonal cold of late summer and autumn.

In addition to the morphological evidence that there are no intergrading forms between the hybrids, very strong evidence is furnished by the high state of fertility in *hybrida pycnella* and *hybrida tortuosa*, which practically show no variability in this respect; and the quite complete self-sterility of *hybrida nutella*.

THE F₂ GENERATIONS

The behavior of these hybrids in the F₂ generation has been studied in all except *hybrida nutella*, which is self-sterile. Thus far the F₂ is obtained only when the hybrid is pollinated by some other form or species. *Hybrida pycnella* and *hybrida tortuosa* are fixed in the first generation, and therefore breed true, the F₂ generation being exactly like the F₁. They will probably continue to breed true in succeeding generations (*pycnella* has been tested to the 3rd generation). In this respect these two hybrids follow the general rule applying to most of the hybrids in the genus *Oenothera* (section *Onagra*) as discovered by DEVRIES (1903, 1911, 1913).

The behavior of the fourth hybrid in the 2nd generation is very peculiar. The F₂ generation of *hybrida tortuella* was first obtained in the summer of 1915 in a number of plants which were grown as annuals: the mature rosette stage was therefore not obtained. The plants presented great variations, apparently none of them assignable strictly to any of the types represented by the two parents or the other three hybrids. No special study was made of these different types partly because the number of other cultures requiring attention made impossible the necessary critical examination of these new types. The result was such a surprising contrast with the behavior of the other three hybrids, it seemed desirable that the culture should be repeated. This was deemed important not only for the purpose of eliminating the possibility of an error in the 1915 cultures, but also that the complete life cycle might be studied in cultures of the plants grown as biennials. Several individuals of the *hybrida tortuella* appeared in the 1915 F₁ generations of reciprocal crosses between *nutans* and *pycnocarpa*, so that there was an opportunity of studying the behavior of this hybrid from both sides of the cross. Flowers were not bagged to save protected seed until quite late in the season. The amount of seed saved was small. As a result of this together with rather scant germination, probably because of immaturity, the number of seedlings obtained was small.

The young plants in 2½-inch pots, bearing 4-5 leaves, were transplanted to the garden near the middle of July 1916. During August the rosettes began to show differences. By September the rosettes were well formed and the variations were very striking. The variations relate to size of the rosette, width of the leaf, edge character, color of the mid-vein, form, crinkledness, etc. In 23 rosettes 9 different types are represented, only one of them approaching the rosette character of *hybrida tortuosa*. These different types of rosette have been photographed and

noted. The further account of them is reserved until the mature plants can be studied in 1917.

BACK- AND INTER-CROSSES OF THE HYBRIDS *PYCNELLA*, *NUTELLA* AND *TORTUOSA*

Further experiments on the interaction of the "factors" present in *Oenothera nutans* and *Oe. pycnocarpa* were undertaken by making all the possible back- and inter-crosses of the three hybrids, *pycnella*, *nutella* and *tortuosa*. The fourth and rare hybrid, *tortuella*, was not included in these experiments for the reason that *tortuella* was at first supposed to be merely a green-stemmed form of *tortuosa*, in which the factor for red stem color was temporarily suppressed, and that it might appear again in the F_2 . It was only after the completion of the back- and inter-crosses of the three other hybrids, that the discovery was made, that the genotypic constitution of *tortuella* was fundamentally different from that of *tortuosa*, resulting in a breaking up into numerous types in the F_2 generation. Some preliminary cultures were made in 1914. These were repeated in 1915 along with the cultures of the remaining back- and inter-crosses.

From the cultures of 1914 it was learned that in the reciprocal back-crosses of *pycnella* with *pycnocarpa*, only one type appeared in the progeny. When *pycnocarpa* was the mother and *pycnella* the pollen parent, the entire progeny was identical with *pycnella*. When *pycnella* was the mother and *pycnocarpa* was the pollen parent, all the progeny was identical with *pycnocarpa*. That is, in the reciprocal crosses between *pycnocarpa* and *pycnella* patrocliny prevailed. But when *nutella* was used in any of the crosses, splitting into two or more types usually occurs. The selective hybrid *pycnella* inherits the greater number of its characters from the *pycnocarpa* parent (furrowedness and lack of crinkledness of the leaves, green stem and all flower characters). This in a large measure, perhaps, accounts for patrocliny as a result of the reciprocal crosses. The segregate hybrid *tortuosa* inherits the greater number of its characters from the *nutans* parent (convexity and crinkledness of the leaves, red stem and all flower characters). The expectation was that reciprocal crosses between *nutans* and *tortuosa* would also result in patrocliny and this expectation was confirmed in the result. The results of all the back- and inter-crosses will not be described in detail, but are given in tables 2 to 9. The F_1 cultures of 1913-1914, and 1915, are combined in tables 2 and 3. The back- and inter-crosses listed in tables 4 to 9 were grown in 1915 unless otherwise indicated.

TABLE 2

*F*₁ generation of *Oenothera nutans* × *Oe. pycnocarpa* showing the splitting into the 4 hybrid types (1 = *pycnocarpa*; 2 = *nutans*).

2 × 1 (1913-1914) Total number plants *F*₁ = 118

	<i>Nutella</i>	<i>Pycnella</i>	<i>Tortuosa</i>	<i>Tortuella</i>
Annuals	35	10	0	0
Biennials	27	24	21	1
Total	62	34	21	1

2 × 1 (1915) Total number plants *F*₁ = 154

Annuals	140	10	2	2
Grand total	202	44	23	3 = 272

TABLE 3

*F*₁ generation of *Oe. pycnocarpa* × *Oe. nutans*, showing the splitting into 3 hybrid types.

(1 = *pycnocarpa*; 2 = *nutans*.)

1 × 2 (1913-1914) Total number plants *F*₁ = 51

	<i>Nutella</i>	<i>Pycnella</i>	<i>Tortuosa</i>	<i>Tortuella</i>
Annuals	4	9	0	0
Biennials	2	36	0	0
Total	6	45	0	0

1 × 2 (1915) Total number plants *F*₁ = 213

Annuals	49	163	0	1
Grand total	55	208	0	1 = 264

TABLE 4

Back-crosses of hybrida nutella with the parents (1 = pycnocarpa, 2 = nutans).

74 = <i>Nutella</i> (2 × 1) × 2 =	$\left\{ \begin{array}{l} \textit{Nutans} \\ \textit{Pycnella} \end{array} \right.$	$\left. \begin{array}{l} 69 \\ 53 \end{array} \right\}$	Total 122
75 = <i>Nutella</i> (1 × 2) × 2 =	<i>Nutans</i>		Total 128
58 = 2 × <i>Nutella</i> (2 × 1) =	$\left\{ \begin{array}{l} \textit{Nutella} \\ \textit{Pycnella} \end{array} \right.$	$\left. \begin{array}{l} 50 \\ 2 \end{array} \right\} \begin{array}{l} *8 \\ 6 \end{array}$	Total 66
57 = 2 × <i>Nutella</i> (1 × 2) =	$\left\{ \begin{array}{l} \textit{Nutella} \\ \textit{Pycnella} \end{array} \right.$	$\left. \begin{array}{l} 90 \\ 8 \end{array} \right\}$	Total 99
Mutant =	<i>Gracilis dwarf</i>	1	
73 = <i>Nutella</i> (2 × 1) × 1 =	$\left\{ \begin{array}{l} \textit{Pycnocarpa} \\ \textit{Nutella} \end{array} \right.$	$\left. \begin{array}{l} 56 \\ 2 \end{array} \right\} \begin{array}{l} *22 \\ 9 \end{array}$	Total 96
Toothed stem leaves	<i>Tortuosa</i>	7	
52 = 1 × <i>Nutella</i> (2 × 1) =	<i>Nutella</i>		Total 118
51 = 1 × <i>Nutella</i> (1 × 2) =	$\left\{ \begin{array}{l} \textit{Nutella} \\ \textit{Tortuosa} \end{array} \right.$	$\left. \begin{array}{l} 25 \\ 1 \end{array} \right\}$	Total 26

* The numbers in the second column of 58 and 73 were cultures of 1914.

TABLE 5

Back-crosses of hybrida pycnella with the parents (1 = pycnocarpa 2 = nutans).

61 = <i>Pycnella</i> (2 × 1) × 1 =	<i>Pycnocarpa</i>	156	Total 156
60 = <i>Pycnella</i> (1 × 2) × 1 =	<i>Pycnocarpa</i>	52	Total 52
53 = 1 × <i>Pycnella</i> (2 × 1) =	<i>Pycnella</i>	75	Total 75
(1914) 1 × <i>Pycnella</i> (1 × 2) =	<i>Pycnella</i>	25	Total 25
62 = <i>Pycnella</i> (2 × 1) × 2 =	$\left\{ \begin{array}{l} \textit{Nutella} \\ \textit{Pycnella} \end{array} \right.$	$\left. \begin{array}{l} 13 \\ 93 \end{array} \right\}$	Total 106
(1914) <i>Pycnella</i> (1 × 2) × 2 =	$\left\{ \begin{array}{l} \textit{Nutella} \\ \textit{Pycnella} \end{array} \right.$	$\left. \begin{array}{l} 3 \\ 18 \end{array} \right\}$	Total 21
54 = 2 × <i>Pycnella</i> (2 × 1) =	$\left\{ \begin{array}{l} \textit{Nutella} \\ \textit{Pycnella} \\ ? \end{array} \right.$	$\left. \begin{array}{l} 90 \\ 6 \\ 26 \end{array} \right\}$	Total 122
55 = 2 × <i>Pycnella</i> (1 × 2) =	$\left\{ \begin{array}{l} \textit{Nutella} \\ \textit{Pycnella} \end{array} \right.$	$\left. \begin{array}{l} 20 \\ 1 \end{array} \right\}$	Total 21

TABLE 6

Back-crosses of hybrida tortuosa with the parents (1 = pycnocarpa, 2 = nutans).

68 = <i>Tortuosa</i> (2 × 1) × 2 = <i>Nutans</i>	108	Total	108
56 = 2 × <i>Tortuosa</i> (2 × 1) =	$\left\{ \begin{array}{l} \textit{Tortuosa} \\ \textit{Tortuella} \end{array} \right.$	$\left\{ \begin{array}{l} 23 \\ 2 \end{array} \right.$	Total 25
67 = <i>Tortuosa</i> (2 × 1) × 1 =	$\left\{ \begin{array}{l} \textit{Nutella} \\ \textit{Pycnocarpa} \\ \text{or} \\ \textit{Pyncnella} \end{array} \right.$	$\left\{ \begin{array}{l} 28 \\ 1 \end{array} \right.$	Total 29
50 = 1 × <i>Tortuosa</i> (2 × 1) =	$\left\{ \begin{array}{l} \textit{Nutella} \\ \textit{Pyncnella} \end{array} \right.$	$\left\{ \begin{array}{l} 63 \\ 85 \end{array} \right.$	Total 148

TABLE 7

Inter-crosses of hybrida nutella and hybrida tortuosa (1 = pycnocarpa, 2 = nutans).

76 = <i>Nutella</i> (2 × 1) × <i>Tortuosa</i> (2 × 1) =	$\left\{ \begin{array}{l} \textit{Tortuosa} \\ \textit{Pycnocarpa} \end{array} \right.$	$\left\{ \begin{array}{l} 17 \\ 46 \end{array} \right.$	Total 63
72 = <i>Nutella</i> (1 × 2) × <i>Tortuosa</i> (2 × 1) =	<i>Pycnocarpa</i>	5	Total 5
(Numbers too small)			
69 = <i>Tortuosa</i> (2 × 1) × <i>Nutella</i> (2 × 1) =	$\left\{ \begin{array}{l} \textit{Nutella} \\ \textit{Pycnocarpa} \\ \textit{Nutans} \end{array} \right.$	$\left\{ \begin{array}{l} 120 \\ 5 \\ 2 \end{array} \right.$	Total 127
70 = <i>Tortuosa</i> (2 × 1) × <i>Nutella</i> (1 × 2) =	<i>Nutella</i>	10	Total 10

TABLE 8

Inter-crosses of hybrida nutella and hybrida pyncnella (1 = pycnocarpa, 2 = nutans).

78 = <i>Nutella</i> (1 × 2) × <i>Pyncnella</i> (2 × 1) =	$\left\{ \begin{array}{l} \textit{Pyncnella} \\ \textit{Nutans} \\ \textit{Nutella} \end{array} \right.$	$\left\{ \begin{array}{l} 90 \\ 29 \\ 1 \end{array} \right.$	Total 120
65 = <i>Pyncnella</i> (2 × 1) × <i>Nutella</i> (2 × 1) =	<i>Nutella</i>	18	Total 18
(1914) — <i>Pyncnella</i> (1 × 2) × <i>Nutella</i> (2 × 1) =	<i>Nutella</i>	34	Total 34

TABLE 9

Inter-crosses of hybrida tortuosa and hybrida pycnella (1 = pycnocarpa, 2 = nutans).

$72 = Tortuosa (2 \times 1) \times Pycnella (1 \times 2) =$		$\left\{ \begin{array}{ll} Nutella & 23 \\ Tortuosa ? \text{ or } Nutans & 16 \end{array} \right\}$	Total 39
$71 = Tortuosa (2 \times 1) \times Pycnella (2 \times 1) =$		$\left\{ \begin{array}{ll} Nutella & 62 \\ Tortuosa \text{ or } Nutans & 43 \end{array} \right\}$	Total 105
$64 = Pycnella (2 \times 1) \times Tortuosa (2 \times 1) =$		$\left\{ \begin{array}{ll} Nutella & 54 \\ Pycnocarpa & 58 \end{array} \right\}$	Total 112
$63 = Pycnella (1 \times 2) \times Tortuosa (2 \times 1) =$		$\left\{ \begin{array}{ll} Nutella & 83 \\ Pycnocarpa & 25 \\ Tortuosa ? \text{ or } Nutans & 3 \\ Tortuella & 1 \end{array} \right\}$	Total 112

This result is remarkable in that in the F_1 generation from a cross between two feral, non-mutating species, quadruple hybrids appear in the F_1 generation; one is a blend and self-sterile, but its pollen and egg cells are fertile; two of the selectives are fixed types and breed true, while the fourth hybrid (also selective) breaks up into different types in the second generation. The back- and inter-crosses show, either striking examples of patrocliny, or splitting into two types in some cases, three types in other cases and four types in one case.

In the back-crosses there are 9 cases of patrocliny, but probably only 5 of these are real (numbers 53, 60, 61, 62, 68). The other cases would probably show splitting if the numbers were larger (52, 70, 72, 75). But the position of the parents in the formula for No. 75, on the principle of an iterative cross (see DEVRIES, 1913, p. 94) may influence the predominance of *nutans* in the cross *nutella* $(1 \times 2) \times 2 = nutans$. In the formula in Nos. 60 and 68 the dominance of the extremes is in accordance with the expectation in double reciprocal crosses of DEVRIES, and so, in No. 61 for the expectation of the iterative cross. In other cases, however, the result, even where patrocliny is present, is not in accordance with the laws discovered by DEVRIES. This is in great part due to the fact that the F_1 splitting into several distinct types occurs on both sides of the reciprocal crosses, rather than patrocliny.

In the back-crosses there are at least 5 cases of patrocliny, 10 cases of splitting into 2 types, and 4 cases of splitting into 3 types. In the inter-crosses there are 2 cases of patrocliny, 3 cases of splitting into 2 types, 1 of splitting into 3 types, and 1 of splitting into 4 types.

But in all of the back- and inter-crosses no new types (with a single exception) appear, they all conform to one or other of the six types, the primary parental types, or one or more of the four F_1 hybrid types. The single exception is a mutant of the dwarf *gracilis* type.

THE BEHAVIOR OF *OENOTHERA NUTANS* AND *OE. PYCNOCARPA* COMPARED WITH
OTHER WILD SPECIES OF *OENOTHERA*

DEVRIES (1913, pp. 30-59) has shown that the production of but one form of hybrid in the first generation of a cross between old, or wild species of *Oenothera* (section *Onagra*) is the general rule. But the hybrids from reciprocal crosses are often different in type (DEVRIES, 1903, p. 471; 1913, p. 30). The hybrids in these reciprocal crosses often resemble the pollen parent strongly, i. e., they are strongly patroclinous (*Oc. biennis* \times *muricata*, etc.). The parents of such crosses he terms *heterogamous* species. A few of the wild species he has shown to be *isogamous*, i. e., the single hybrids of reciprocal crosses are identical (*Oe. Hookeri*, *Cockerelli* and *strigosa*, see DEVRIES, 1913, p. 59). The behavior of *Oc. nutans* and *pycnocarpa* in reciprocal crosses does not conform to either of the types of behavior found by DEVRIES to be characteristic of the heterogamous or isogamous species which he has studied. So far as the vegetative characters are concerned patrocliny can not be ascribed to either of the hybrids, for the characters are either blended (in *hybrida nutella*) or selected and distributed about equally from the parents to two of the selective hybrids (*pycnella* and *tortuosa*).

In the selectives, while certain characters resemble those of one parent, other characters resemble those of the other parent and it is difficult to say which set of characters dominates. But even if one hybrid should be judged to indicate patrocliny in one cross, the same hybrid appears in the reciprocal cross where it would be a case of matrocliny for the same hybrid. While the behavior of *pycnocarpa* and *nutans* in reciprocal crosses is similar to that of isogamous species, in that the hybrid production in one cross is the same in the reciprocal cross,¹¹ there are three to four different hybrids instead of one, as in the wild isogamous species like *Oc. Hookeri*, *Cockerelli* and *strigosa*. Nevertheless, since the same types of hybrids are produced on each side in reciprocal crosses, it seems to indicate that the same heritable characters are transmitted in the pollen and egg cells. In this respect the parents (*pycnocarpa* and *nutans*) behave like isogamous species, but differ from such isogamous species as *Oe. Hookeri*, *Cockerelli* and *strigosa* in the production of several distinct

¹¹ Only 3 hybrid types have thus far appeared in the cross *Oc. pycnocarpa* \times *nutans*.

hybrid types, all of which, in their vegetative characters are blends or recombinations of the parental characteristics.

INTERPRETATIONS OF SPLITTING IN THE FIRST GENERATION

Selection of characters in the zygote versus Mendelian segregation

The selection and blending of the factors which make up the constitution of the two parents (*nutans* and *pyncocarpa*), into the three selective hybrids (*pyncella*, *tortuosa*, and *tortuella*, and the blend hybrid (*nutella*), occurs in the zygote or fertilized egg. Therefore it is of a very different type from that which takes place in Mendelian segregation. No such qualitative division as occurs in the gonotokonts, providing for the segregation of factors in Mendelian hybrids, is known to take place in the fertilized egg, and can not be invoked to explain zygotic selection.

Very little is known of the cytological processes in the fertilized egg of plants, so far as it relates to the more critical stages in the organization of the nuclear figure for the first division, and the behavior of the paternal and maternal chromosomes in the organization of a working relation in the new diploid nucleus. GUIGNARD (1890) describes and figures the spindle for the first division of the fertilized egg in *Lilium Martagon*. It is preceded by a double gnarl stage representing the paternal and maternal nuclear chromatin skeins. But the formation and association of the paternal and maternal chromosomes in the zygote was not observed. In *Pinus Strobus* MARGARET C. FERGUSON (1901, 1904) has shown that while the sperm and egg nuclei are in close contact the spindle is organized between them, while the paternal and maternal chromosomes form from the chromatin net-work of the sperm and egg respectively and move to the nuclear plate of the spindle. In two successive divisions the paternal and maternal chromosomes are formed in separate groups. But their final arrangement and relation, as cell wall formation and the morphogenic processes begin in the embryo, were not determined. STRASBURGER (1904, p. 20) attempted to study the relation of the paternal and maternal chromosomes in the fertilized egg of *Funkia* and *Galtonia*, where the chromosomes are of different sizes, but was unable to accomplish the desired result because of the rarity of seed formation. In the fertilized egg of *Iris Siberica* and *Triticum vulgare*, he discovered nothing unusual. The difficulties met with in the study of the cytological processes of the first division of the fertilized egg in plants appear to be very great. But it is an important and critical stage in the life cycle of plants, which deserves investigation.

Is the production of these quadruple hybrids due to the mutating condition of one of the parents?

The appearance of quadruple hybrids in the F_1 generation of a cross between two wild, non-mutating species is a rather unique phenomenon. Twin hybrids regularly appear in crosses of *Oe. Lamarckiana* or certain of its derivatives, with certain wild, non-mutating species of *Oenothera*, as demonstrated by DeVRIES (1907, 1909, 1913). These crosses are termed by DeVRIES "*mutation crosses*." Triple and even quadruple hybrids appear in certain mutation crosses. But heretofore triplets or quadruplets in the F_1 generation have only appeared when the mutant parent is an inconstant race and tends to repeat itself in crosses.

Oenothera nutans and *Oe. pycnocarpa* are constant, non-mutating feral species. The progeny is remarkably uniform, has been grown in several successive generations, presents a high degree of seed and pollen fertility, breeds true and the gametes are uniform. The two species have appeared each year, in typical form, in the same locality where they were discovered in 1909.

The number of plants grown in successive generations is shown in the following table.

TABLE 10

	<i>Nutans</i>	<i>Pycnocarpa</i>
1911-12	100	50
1913-14	75	19 ⁸
1915-	152	70
1916	15	20

In 1916 very few of the seedlings grown in the pans were transplanted to the garden, since only a few plants were desired to raise seed and for a few pollination experiments. Each year the percentage of seed germination was high though the actual percentage was not determined by counting. The seeds were sown in good potting-room soil in seed pans 4-6 inches in diameter. The seeds were then covered with a rather thick layer of pure sand or fine gravel, so that the cover would not cake. Gravel and coal ashes are favorite substrata for *oenotheras*. The soil was kept well watered and a favorable temperature was maintained. Where an abundance of seed was sown, large numbers of seedlings developed so that in most cases they were closely packed in the pans. In such cases not all of the seedlings were transplanted to the garden, but great care was taken to select from among all sizes of seedlings in the

pan, in order to be certain that different types were not represented by the smaller and younger seedlings. The evidence therefore is very strong that *Oenothera nutans* and *Oe. pycnocarpa* in cultures are pure lines, notwithstanding the unwarranted assumption by DAVIS (1916, p. 245) that they are of "doubtful genetic purity."

This assumption appears to be based on the very questionable hypothesis that, since twin, triple or quadruple hybrids appear in the F_1 generation of a cross, one or both of the parents are mutating species and that a mutating species is *per se* genotypically impure.¹² Numerous cases are known in pure line work, where mutations have arisen from a pure line. N. H. NILSSON of the Swedish Experiment Station at Svalöf has described a mutant with stiff straw and stout heads from a pure line of wheat (see JOHANSEN 1909, p. 443). According to DEVRIES (1907 b, p. 85) the workers at "Svalöf are satisfied that real mutations as well as accidental crosses are occurring in their pure pedigree-cultures, from time to time." JOHANSEN (1909, p. 457) relates the appearance of a mutation from one of his pure lines of beans. He also cites other cases of mutations from pure lines in animals as well as in plants. The evidence of their appearance in pure lines is abundant.

No mutations in the pure lines of *Oenothera nutans* and *Oe. pycnocarpa* have appeared, though several mutants have been thrown in my cultures of *Oenothera Lamarckiana* where the number of individuals in the culture varied from 75 to 100. Among all the crosses (parental, back- or inter-crosses) only one mutant has appeared in the hybrid progeny of *nutans* and *pycnocarpa*. This was a *gracilis* dwarf mutant in the back-cross *nutans* \times *nutella* (1×2).¹³ But the appearance of a mutant is not an indication that the line is impure, and furthermore this mutant did not appear in the direct line of either parent, but in one of the back-crosses.

The appearance of triple and quadruple hybrids in the F_1 generation of reciprocal crosses between *Oe. nutans* and *Oe. pycnocarpa* can not be explained on the basis of the interesting theory of "mutation crosses" in the same sense as interpreted by DEVRIES. We have no evidence that the species are mutating, and furthermore the four hybrids of the F_1 generation are very different from the twin hybrids of DEVRIES's mutation crosses. In mutation crosses, according to DEVRIES, there is a splitting of the entire constitution (gametic) so that all the vegetative char-

¹² JOHANSEN says (1909, p. 448) that the oft repeated conjecture that mutations indicate the hybrid nature of the parent has little worth.

¹³ See table 4.

acters are split, not selected as in *pyncella*, *tortuosa* and *tortuella*, nor equally blended as in *nutella*.

The four different hybrid types in the F_1 generation of crosses between *Oc. pyncocarpa* and *Oc. nutans* differ from the mutation crosses described by DEVRIES in another respect. In the mutation crosses triplets and quadruplets are formed only when the mutant parent is an inconstant race, for example, *Oc. lata*, which is nearly pure female, though rarely *lata*-like forms which produce pollen appear in the F_1 when *lata* is crossed with other species (DEVRIES 1913, p. 245). When *Oc. lata* is pollinated with *Oc. Hookeri*, *Cockerelli*, *bicnnis Chicago*, etc., the splitting in the first generation produces the twins, *lacta* and *velutina*, and in addition a third form which is *lata* repeated, but slightly modified. The most common modified form of this *lata* arising by splitting in the first generation of a cross shows a resemblance to *lacta* forms and is called *lata-lacta*. Besides the splitting in the F_1 generation into twins, *lacta* and *velutina*, the inconstant race repeats itself. The repeated form is modified by *lacta* characters (the "triplet") and rarely a small percentage is modified by the *velutina* characters ("quadruplet"). This is strong additional evidence that the triple and quadruple hybrids in the first generation of crosses between the wild species *Oc. pyncocarpa* and *Oc. nutans*, represent a type of splitting different from that manifested in the mutation crosses of DEVRIES, and does not appear capable of interpretation on the same hypothesis.

The three hybrids, *pyncella*, *tortuosa* and *tortuella*, have been spoken of as selective hybrids, since certain parental factors are selected in the zygote, and the characters they represent are developed to their full expression, other factors being either eliminated or subordinated, so that they do not enter into the composition, at least the phenotypic composition, of the new types. If they were true segregates in their genotypic constitution, the interesting question would arise as to how this segregation of certain factors in the zygote, and the elimination or subordination of others, takes place. In Mendelian segregation the mechanism of allotypic division in the gonotokonts is generally accepted as furnishing a means for the segregation. But no such mechanism of nuclear divisions occurs in the zygote. The stage of fecundation and the first nuclear division in the zygote is a critical period in the ontogeny of the individual, and particularly so in the F_1 zygote of crosses.

If there is an elimination of certain factors in the composition of these selective hybrids, we may conceive that it takes place by the shunting to one side, during nuclear division in the zygote, of some of the factor-

bearing material, a phenomenon, perhaps, similar to merogony as recently defined by GOLDSCHMIDT (1916). GOLDSCHMIDT (1912) sought to find a cytological basis for patrocliny exemplified in deVRIES's crosses of *Oenothera biennis* and *Oe. muricata*, etc., where the F_1 hybrid in its vegetative characters is nearly or quite identical with the pollen parent. His first cytological interpretation of this phenomenon predicated the degeneration of the egg cell, there being no fusion of the sperm and egg, so that the embryo was developed exclusively from the male cell. According to his recent studies on material of reciprocal crosses of *Oc. atrovirens* and *Oc. venosa* there is a fusion of the sperm and egg cells, but during the first division of the zygote the chromosomes from the egg are eliminated from the daughter nucleus of the embryo cell and degenerate in the cytoplasm. Such a process, if the hereditary factors are carried by the chromosomes alone, would result in the complete reproduction of the pollen parent in the F_1 , not modified by the ovule parent. But in cases of patrocliny among the *Oenotheras*, where the flower and inflorescence characters are different in the two parents, the F_1 plants, while very strongly resembling the pollen parent in vegetative characters, often resemble the ovule parent more or less strongly in the inflorescence.

The fact that the patroclinous F_1 generation in such *Oenothera* crosses is more or less modified by the maternal characteristics, especially in the inflorescence, indicates that factor-bearing material is contributed to the F_1 generation by the mother plant of the cross. It should be said, however, that GOLDSCHMIDT (1912) does not commit himself unreservedly to the merogony theory as an explanation of patrocliny in the *Oenotheras*. It appears to me that these cases of patrocliny in the *Oenotheras*, where the hybrid is fixed in the F_1 generation, are examples of *permanent dominance*, such hybrids being *physiological homozygotes*.

Stable and unstable dominance in the hybrids pycnella, tortuosa and tortuella

I have sometimes spoken of these hybrids as "segregate" hybrids, because they at least appear to be segregates in their phenotypic constitution. But I have been led to believe from a study of my *Oenothera* cultures during the past two seasons, that these three hybrids can be classed as cases of selective dominance, though perhaps not in the strict Mendelian sense. If there were a splitting in the F_2 generation, releasing the parent forms in 50 percent of the progeny and forming 50 percent heterozygotes there would be no question that *hybrida pycnella* and *hybrida tortuosa* in the F_1 generation were true Mendelian dominants, for the F_1 hybrids in Mendelian crosses are often intermediates. In each of

these hybrids dominance of parental characters is complete in relation to nearly all the visible characters. But not all of the dominant characters of either hybrid come from a single parent. There is a selection of factors from each parent, a "crossing over" between the linked factors. A certain group of factors is dominant in *pycnella*, while another group of factors is subordinate. The group of subordinate factors in *pycnella* becomes the dominant one in *tortuosa*. Since these *hybrids* are fixed in the F_1 generation they may be considered as cases of fixed or permanent dominance.¹⁴ They are physiological homozygotes.

In support of this interpretation of the genotypic constitution of *pycnella* and *tortuosa* is the fact that in certain of the back-crosses where splitting occurs in the zygote, *nutella* is one of the "segregates." In these back-crosses *nutella* is not one of the parents. This behavior is shown in the following tables: compiled from tables 5 and 6.

TABLE 11

Back-crosses of hybrida *pycnella* with parent *nutans* (2 = *nutans*, 1 = *pycnocarpa*).

62 = <i>Pycnella</i> (2 × 1) × 2 =	$\left\{ \begin{array}{l} \text{Nutella} \\ \text{Pycnella} \end{array} \right.$	$\left\{ \begin{array}{l} 13 \\ 93 \end{array} \right.$	Total 106
(1914) <i>Pycnella</i> (1 × 2) × 2 =	$\left\{ \begin{array}{l} \text{Nutella} \\ \text{Pycnella} \end{array} \right.$	$\left\{ \begin{array}{l} 3 \\ 18 \end{array} \right.$	Total 21
54 = 2 × <i>Pycnella</i> (2 × 1) =	$\left\{ \begin{array}{l} \text{Nutella} \\ \text{Pycnella} \\ ? \end{array} \right.$	$\left\{ \begin{array}{l} 90 \\ 6 \\ 26 \end{array} \right.$	Total 122
55 = 2 × <i>Pycnella</i> (1 × 2) =	$\left\{ \begin{array}{l} \text{Nutella} \\ \text{Pycnella} \end{array} \right.$	$\left\{ \begin{array}{l} 20 \\ 1 \end{array} \right.$	Total 21

TABLE 12

Back-crosses of hybrida *tortuosa* with parent *pycnocarpa* (2 = *nutans*, 1 = *pycnocarpa*).

67 = <i>Tortuosa</i> (2 × 1) × 1 =	$\left\{ \begin{array}{l} \text{Nutella} \\ \text{Pycnocarpa} \\ \text{Pycnella} \end{array} \right.$	$\left\{ \begin{array}{l} 28 \\ 1 \\ 1 \end{array} \right.$	Total 29
50 = 1 × <i>Tortuosa</i> (2 × 1) =	$\left\{ \begin{array}{l} \text{Nutella} \\ \text{Pycnella} \end{array} \right.$	$\left\{ \begin{array}{l} 63 \\ 85 \end{array} \right.$	Total 148

¹⁴ The term *permanent*, or *stable*, *dominance*, relates to the fixity of the type in the F_1 generation of a cross so that if selfed, the type appears in successive generations unchanged. It implies also the permanent recessiveness, latency or subordination of the other factors in the F_1 zygote of the cross which were not activated. In *unstable dominance*, the type appearing in the F_1 generation is not fixed, but splits or shows extraordinary fluctuation in the F_2 . *Selective dominance* relates to the dominance of the active factors in a selective hybrid.

In table 11 it is seen that from the back-crosses of *hybrida pycnella* with parent *nutans*, 270 in all, there appear 126 individuals of *hybrida nutella*. Parent *nutans* and *hybrida pycnella* it will be remembered, both have broad rosette leaves somewhat toothed over the basal portion. The rosette leaves of *hybrida nutella* are intermediate in width and edge character between the broad and toothed leaves of parent *nutans* and the narrow cut leaves of parent *pycnocarpa*. The factor for this character (narrowness and cutness of rosette leaves, and some others also) of *pycnocarpa* must, therefore, be present in *hybrida pycnella* of these back-crosses, but in a latent or "recessive" state. When *hybrida pycnella* is back-crossed with parent *nutans* these latent factors become active in a large percent of the zygotes and the blend *hybrida nutella* appears.

In like manner, as seen from table 12, in the back-crosses of *hybrida tortuosa* with parent *pycnocarpa*, 177 in all, there appear 91 individuals of the blend, *hybrida nutella*. Since both *tortuosa* and *pycnocarpa* have narrow, cut leaves, the factor for width and edge character of the rosette leaves of parent *nutans* (other factors also) must be present in *tortuosa*, but in a subordinate, or "recessive" state.

These back-crosses, therefore, present evidence that in each of the hybrids, *pycnella* and *tortuosa*, certain factors, selected some from one parent, some from the other, are active or dominant¹⁵ in the zygote of the F_1 and the characters they represent are developed to their full expression. The alternative factors are subordinate or "recessive" in each hybrid and become active in a certain percentage of the zygotes of back-crosses. The result of this analysis of the hybrids indicates quite clearly that the gametes of *Oenothera nutans* and *Oc. pycnocarpa* are uniform. It is not necessary to resort to the rather overworked hypotheses of dissimilar gametes in the parents of twin hybrids, nor of those giving a larger number of distinct hybrids in the F_1 generation, except where one of the parents is an inconstant race, as in *Oenothera lata*, etc. The evidence from *Oenothera* cultures points more and more to the conclusion of SHULL (1914) that "a hereditary mechanism must exist in *Oenothera* fundamentally different from that which distributes the Mendelian unit-characters."

¹⁵ SWINGLE (1898, 1913) has proposed a hypothesis for the different types of hybrids appearing in the first generation of interspecific crosses which he calls "zygotaxis." It assumes the chance arrangement of the parental chromosomes in different positions in different zygotes. These positions are maintained throughout the ontogeny. Those chromosomes situated nearer the cytoplasm are better fed and exercise a greater influence on the formative processes in the cell than those more distant. In consequence of the different arrangement in different zygotes, different hybrid types appear.

In *tortuella*, which differs from *tortuosa* in having a green stem instead of a red one, the dominance of the factor composition in the F_1 is not fixed. A breaking-down takes place in the F_2 generation. The complete composition of the individuals of this second generation can not be determined until they come into flower in 1917; but from the types of rosette present it is clear that in *tortuella* certain factors are present in its genetic constitution which are subordinated in the F_1 and only come into play in some of the individuals of the F_2 (breadth and edge character of the rosette leaves for example).

We do not know the behavior of *hybrida nutella* in the F_2 generation, and cannot say whether or not it is a physiological homozygote. It is almost a perfect blend of the two parents. Besides certain features of the inflorescence and fruit spike which differ to some extent from each parent and do not represent an intermediate condition, the petals are more like those of *nutans*, and it might be considered a dominant in the F_1 favoring *nutans*.

Multiple dominance¹⁰ in the F_1 generation of crosses between Oenothera nutans and Oc. pycnocarpa

On this interpretation, then, there are four types of dominance in the F_1 of crosses between *Oc. nutans* and *pycnocarpa*. All four appear when *pycnocarpa* is the pollen parent. Only three have thus far appeared when *nutans* is the pollen parent. Two of these, *pycnella* and *tortuosa* are fixed dominants, and are physiologically homozygous. The genotypic constitution of the F_1 dominant *tortuella* is dissolved in the F_2 . The later history of *nutella* is unknown.

In many cases interspecific crosses are difficult or impossible to obtain. In general this difficulty is greater in proportion to the remoteness of the relationship between the species used in the attempted cross. There is apparently great difficulty in establishing a working relation between the sperm and egg nuclei after their association, whether of a chemical or mechanical nature. The disturbance caused by the entrance of a foreign sperm into the egg should not be overlooked. Chemical, enzymatic and mechanical disturbances result, the effect of which may vary according to the differences in the constitution of the parents used in the cross. The reciprocal shock on the germ cells when they meet in the egg may be sufficient in many cases to break some of the remoter

¹⁰ Multiple dominance relates to the appearance of several distinct hybrid types in the F_1 of a cross, certain factors being completely or partially dominant in each type, the other factors being subordinate, latent, or recessive.

linkages of factors in the parents. Chance then partly determines the new association in the four different hybrid types in the F_1 of *Oe. nutans* \times *pyncocarpa*.¹⁷

All, or nearly all, the active factors of the two parents enter equally active and with the same association, into the constitution of the zygote of the blend, *hybrida nutella*. The effect of the shock merely retards somewhat the organization of a working relation between the sperm and egg nuclei.

In the three other hybrids the effect of the shock is such, that, when the organization of a working relation between the germ cells is formed, certain factors are rendered subordinate or inactive. The shock, to use a figurative expression, shakes up the elements of the composition, "crossing over" occurs, and they fall into new combinations, or alliances, or systems. To some extent chance probably determines the new combinations but there are varying degrees of linkage between certain factors. Among the factors relating to the leaves, linkage is strong in couplets, as width and edge character, convexity and crinkledness, furrowedness and lack of crinkledness. In the case of the flowers the linkage among all the factors of each parent is strong. While the shock breaks the general bond of linkage of the sum total of factors in each species, it does not destroy the linkage present in lesser associations of factors. To some extent chance determines whether one or the other of the "selective" hybrids is formed. In two of these hybrids (*pyncella* and *tortuosa*) the activity or inactivity of the factors is fixed so long as the hybrids are self-fertilized. They breed true in the F_2 and following generations, since they are physiologically homozygous. But patrocliny and splitting occurs in the back- or inter-crosses. In *hybrida tortuella*, when the working relation is established between the factors of the germ cells in the F_1 zygote, the activity or inactivity of certain factors is fixed only for the F_1 generation. The organization of the working relation between the factors is unstable, and breaks down in the second generation into, perhaps, numerous types, as in certain other species hybrids (see BAUR 1911, p. 207). Since some of the types presented in this F_2 generation have the breadth and edge character of the leaves of the parent *nutans*, a character not present in the phenotype of *hybrida tortuella*, its appearance in the F_2 generation of *tortuella* indicates that the *nutans* factor for breadth and toothedness of the rosette leaves was present in *tortuella* but in a subordi-

¹⁷ The result would vary in different species crosses according to the firmness with which the association of factors in either parent held to its genotypic type.

nate condition. In the fixed "selective" hybrids the color of the stem is linked with flower characters in the same way as in the parents.

In *hybrida pycnella* greenness of stem is linked with *pycnocarpa* flowers, in *hybrida tortuosa* redness of the stem is linked with *nutans* flowers. In *hybrida tortuella* this link between color of the stem and flower characters is broken. It is possible that this may be evidence present in the first generation that many of the linkages among factors in the parents are broken, thus rendering the composition of *tortuella* very unstable. This splitting of *hybrida tortuella* in the second generation does not appear to be of the Mendelian type.

One cause of the peculiar behavior of the *Oenotheras* may be that the association, or linkage of factors, is not very strong in the germ plasm, but varies in that respect in different species. The germ plasm is peculiarly sensitive to shock from the meeting of sperm and egg, particularly when there is a genotypic difference between the two germ plasms. This results more or less in interchange, crossing over, dominance, as well as blending, of factors in the zygote, often accompanied by selection of factors into different associations in different zygotes giving rise to more than one hybrid type in the F_1 generation of crosses.

SUMMARY

1. In the F_1 generation of the cross *Oenothera nutans* \times *Oc. pycnocarpa*, four different hybrid types appear which are named as follows: *Oc. hybrida nutella*; *Oc. hybrida pycnella*; *Oc. hybrida tortuosa*; and *Oc. hybrida tortuella*. In the F_1 generation of the reciprocal cross, *Oc. pycnocarpa* \times *Oc. nutans* three hybrid types have appeared which are identical with three of the types named, viz., *nutella*, *pycnella* and *tortuosa*. If the number of the individuals of the F_1 *pycnocarpa* \times *nutans* was very large it is probable that *tortuella* also would appear.

2. *Nutella* is a *blend* hybrid; all the homologous factors of the parents are active and the phenotype is a mean between the two parents, with some exceptions in the inflorescence. Thus far *nutella* has proven absolutely self-sterile, but the pollen and egg cells are highly fertile in back- and inter-crosses, and in reciprocal crosses with other species.

3. *Pycnella* and *tortuosa* are *selective* hybrids. For example, in the F_1 zygote which develops into *pycnella*, all of the factors of the two parents are present. Certain of these factors from each parent are selected in the organization of the working relation between them, and the characters they represent are developed to their full expression, while the other members of the homologous factors remain subordinate.

Tortuosa is organized in a similar way, but the factors which are subordinate in *pycnella* are active in *tortuosa*, and *vice versa*. In phenotypic constitution *tortuosa* and *pycnella* are counterparts of each other.

4. *Pycnella* and *tortuosa* are physiological homozygotes; they are fixed in the first generation, and when selfed they are repeated in the F_2 and succeeding generations.

5. *Tortuella* is also a selective hybrid, but it is not fixed in the F_1 ; when selfed it dissolves in the F_2 into numerous types, some of which show that certain factors which were subordinate in the F_1 are activated in the F_2 .

6. The production of 4 hybrid types in the F_1 is an example of multiple dominance i.e., many dominant types appear. *Pycnella* and *tortuosa* are examples of permanent or stable dominance of factors.

7. In back-crosses there are clearly 5 cases of patrocliny, 10 cases of splitting into 2 types, and four cases of splitting into 3 types.

8. In the inter-crosses there are 2 cases of patrocliny, 3 cases of splitting into 2 types, 1 of splitting into 3 types, and 1 of splitting into 4 types.

9. In all of the back- and inter-crosses no new types (except a dwarf *gracilis*) appear; they all conform to one or other of the six types, the primary parental types, or one or more of the four F_1 hybrid types.

10. In the back-crosses of the selective hybrid *pycnella* with parent *nutans*, and of the selective hybrid *tortuosa* with parent *pycnocarpa*, the blend hybrid *nutella* appears in a high percentage of the progeny. A number of the phenotypic characters of parent *pycnocarpa* are not present in the phenotype of *pycnella*. The factors for these characters, however, must be subordinate or latent in *pycnella* for when crossed with parent *nutans* these subordinate *pycnocarpa* characters are activated in a high percentage of cases and make possible the appearance of the blend *nutella*. Likewise in back-crosses of *tortuosa* and *pycnocarpa*, the subordinate *nutans* factors in *tortuosa* are activated in a high percentage of cases and make possible the appearance of the blend hybrid *nutella*.

11. The analysis summarized in Nos. 5 and 10 indicates that the gametes in the parents *nutans* and *pycnocarpa* are uniform.

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INHERITANCE OF A MOSAIC PERICARP PATTERN COLOR OF MAIZE¹

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INTRODUCTION

Selection experiments for the purpose of testing JOHANNSEN's pure line hypothesis have given radically different results. In some cases selection within the pure line has served to isolate new types in which the character studied is progressively changed in the direction of the selection (JENNINGS 1916). In other experiments continued selection of plus and minus variates has not altered the mean of the progeny to any appreciable extent. This would indicate that some characters are in a much more stable condition than others. Mosaic or variegated pattern colors are examples of characters which exhibit a high degree of variability. For this reason carefully planned selection experiments with this class of characters should be of especial interest. The purpose of this paper is to describe experiments with a mosaic pericarp pattern color of maize.

PREVIOUS STUDIES ON VARIEGATION

DE VRIES (1910, pp. 113-160) carried on a number of experiments with variegated flowers. A brief summary of his work with *Antirrhinum*

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majus luteum striatum shows the general nature of his results. He found the variety *striatum* to be an inconstant race. There was found to be a continuous range of variation from narrow- to broad-striped forms. The narrowly striped forms gave only a small percentage of self red types (from 2 to 5). The broadly striped individuals gave a percentage of from 11 to 42 self red individuals. The self red form obtained from variegated parentage gave a progeny of about 25 percent variegated and 75 percent red. This variegated type is an example of an "eversporting variety." This term is applied to a race "*which produces in every generation a fairly constant proportion of atavists.*"

CORRENS (1910) reported a study of the inheritance of the self green condition which appeared as a bud sport on variegated-leaved plants of *Mirabilis*. The green branches gave a progeny of about 75 percent green and 25 percent variegated. Of the 75 percent green plants approximately one-third bred true for self green and two-thirds again gave 75 percent green and 25 percent variegated.

EAST and HAYES (1911) report the case of an ear which was found in a field of dent maize of unknown parentage. This ear had seeds with a red pericarp on one side and seeds which were white or had a narrow red stripe on the other side. As no other red ears appeared in the field, it was supposed that this ear was nearly all pollinated by white. The red seeds gave a progeny of 50 percent red ears and 50 percent white ears. The white and striated seeds gave 50 percent ears with some striated seeds and 50 percent with white seeds. The result was explained on the basis that the plant due to produce a red ear varied somatically so that a part of the ear was red the other part white and striated.

EMERSON (1914) reports experiments with a recurring somatic variation in variegated ears of "Calico" dent corn, *Zea mays indentata*.^{*} The variegated condition is the result of stripes of red occurring on the pericarp of the seeds, the remaining area being colorless or showing a sort of washed out red. In some cases there were seeds with a colorless pericarp and also seeds with self red pericarp scattered over the same ear. Rarely, freak ears were found with a patch of self red or nearly self red grains. The number and width of the red stripes were very variable, the range of variation being from ears with only a single narrow stripe on one seed to ears with a few seeds striped, the remaining seeds having a self red pericarp.

Self-fertilized ears of this variegated race were obtained and seeds with various amounts of red were selected. The results showed that the more red there was in the seed planted the larger the percentage of red

ears in the progeny. The pollination of an uncolored race by the variegated race gave about 12 percent self red ears which showed that some of the male gametes of the variegated race carried factors for self red.

The red ears obtained from self-fertilized seed of homozygous variegated ears behaved as if they were F_1 crosses between red-eared and variegated-eared races, and gave a progeny with a ratio of approximately three self red ears to one variegated ear. In later generations a portion of the self red ears bred true.

EMERSON concludes that the fact that variegated plants occasionally produce self red ears is not in general to be taken as an indication that the variegated plants in question are heterozygous, but that such behavior seems to be inseparably associated with variegation. His results are explained on the hypothesis that in a homozygous race, one of the factors for variegation V changes to a factor for self color or S . No attempt is made to explain the cause of this change, although the author mentions the possibility that this is due to changing metabolic processes in the maturing plant, or to external influences, or to a quality inherent in the factor itself. EMERSON shows that the results of DE VRIES, CORRENS, and EAST and HAYES, can be explained in a similar manner.

The recent experiments by STOUT (1915) on selection of somatic variations show that variegated pattern colors of *Coleus* are very variable. He found that bud variations were common and the conclusion was reached that "in *Coleus* asexual and sexual reproduction were not fundamentally different in respect to the extent and range of variation." Sexual reproduction produced all types of variation in F_1 , which shows that the characters dealt with were heterozygous. No evidence was found of the somatic segregation of invariable pattern factors. This was thought to be due to the fundamental relations between the chemical compounds involved.

On submitting this paper for publication the author learned that a further study with variegated pattern colors of dent maize had been made by EMERSON and would appear in an early number of *GENETICS*. These recent investigations (EMERSON 1917) were made by pollinating the progeny of variegated maize races by colorless strains. A careful separation of the seeds of the ears thus obtained was made. "Self-colored, partly self-colored, variously variegated and colorless seeds from variegated parent ears, thus pollinated, have given progenies containing a percentage of self-colored ears roughly proportional to the amount of self color in the seeds planted."

Evidence is given for two, and possibly more, distinctly different types

of variegation. The two types which were clearly demonstrated were called very light variegated and medium variegated. The very light variegated type, V_1V_1 , "has little red (or brown) color—few more or less fully self-colored seeds and few even that are prominently striped with color—because the factor concerned changes to a factor for self color comparatively rarely." The medium variegated type has more self-colored seeds because the factor for medium variegation, V_mV_m , more frequently changes to the self color condition.

EMERSON concludes that there is a series of nine or ten multiple allelomorphs to which variegation belongs and that these various factors are a result of several mutations from an original factor. Some of these factors mutate frequently, others rarely and still others have never been observed to mutate. The more distinct types of variegation are inherited in a simple Mendelian way, without apparently any evidence of contamination.

EMERSON has used the term sporophytic variation in the place of somatic variation for that class of changes which occur in meristematic cells from which later arise the germ cells as well as the somatic tissues in which the variation is exhibited.

THE MATERIAL USED AND METHOD OF ATTACK

The material used for the present study belongs to the subspecies *Zea mays indurata*. It was known as "Brindle flint" and did not prove to be homozygous for the character from which it takes its name. The mosaic pericarp is formed by either narrow or broad red stripes extending irregularly from the point of attachment of the silk. The ear appears as dark, medium, or light, mosaic, with the variation in number and width of these red slashes.

As the material did not breed true for the character to be studied (1909-'10) it was decided to attempt the production of homozygous races by self-fertilization.

The field technique has been described in a previous publication (EAST and HAYES 1911). At this time a determination was made of the degree of experimental error during pollination. Twenty-five ears were handled in the same way as if pollination was to be made, with the exception that no pollen was applied. Of these twenty-five ears 16 produced no seeds; three ears produced one seed each; four ears produced two seeds each; while one ear produced five seeds. Thus the experimental error is probably less than one seed per ear with a maximum error of five to six seeds per ear.

For the first six years (1909-1914) the work was carried on at the CONNECTICUT EXPERIMENT STATION. Since 1915 it has been conducted at the MINNESOTA EXPERIMENT STATION.

The author wishes to acknowledge his indebtedness to Mr. C. D. HUBBELL and Mr. A. F. SCHULTZ of the CONNECTICUT EXPERIMENT STATION and Mr. P. J. OLSON of the MINNESOTA EXPERIMENT STATION for aid in the field work involved.

CONTINUOUS SELECTION FOR TYPE

The first two years of the experiment (1909-10) showed that all ranges of variation from dark, heavily striped ears to colorless-pericarp ears could be obtained. It is worthy of note that no self red ears appeared in either year in a total progeny of 188 ears.

From 1911 to 1916 selection experiments were carried on for the purpose of isolating pure types. The parental ears used were self-pollinated in all cases. Eight classes were used for the description of the progeny according to the amount of variegation of the ears obtained. These classes for pericarp color were: Self red, deep mosaic some seeds self, deep mosaic, medium mosaic, light mosaic, few seeds striped, very slight pattern, and colorless. In addition a record of bud sports was kept showing the somatic variation involved. The self red class consisted of ears in which all seeds were uniformly covered with a red pericarp. In the deep mosaic some seeds self class were placed all ears in which a portion of the seeds were very heavily striped, the remaining seeds having a self red pericarp. The classes, deep mosaic, medium mosaic and light mosaic were used for those ears in which a considerable portion of the seeds were striped with deep red. The number and width of these stripes determined the class in which ears were placed. The class, few seeds striped, consisted of ears in which from 1 to 50 seeds had a few stripes of deep red on the pericarp. The class, very slight pattern, consisted of ears which showed no deep red stripes on the pericarp, but which nevertheless seemed to have a slight color in the pericarp. Microscopical examination showed some reddish coloration in a portion of the cells while other pericarp cells appeared to have no coloring matter. The colorless class consisted of ears in which there appeared to be no color in the pericarp.

It is realized that in a number of these classes no sharp distinction exists. For example the classes deep mosaic, medium mosaic and light mosaic grade into each other. There is also some difficulty in separating the classes, very slight pattern, and colorless. Those ears in which this

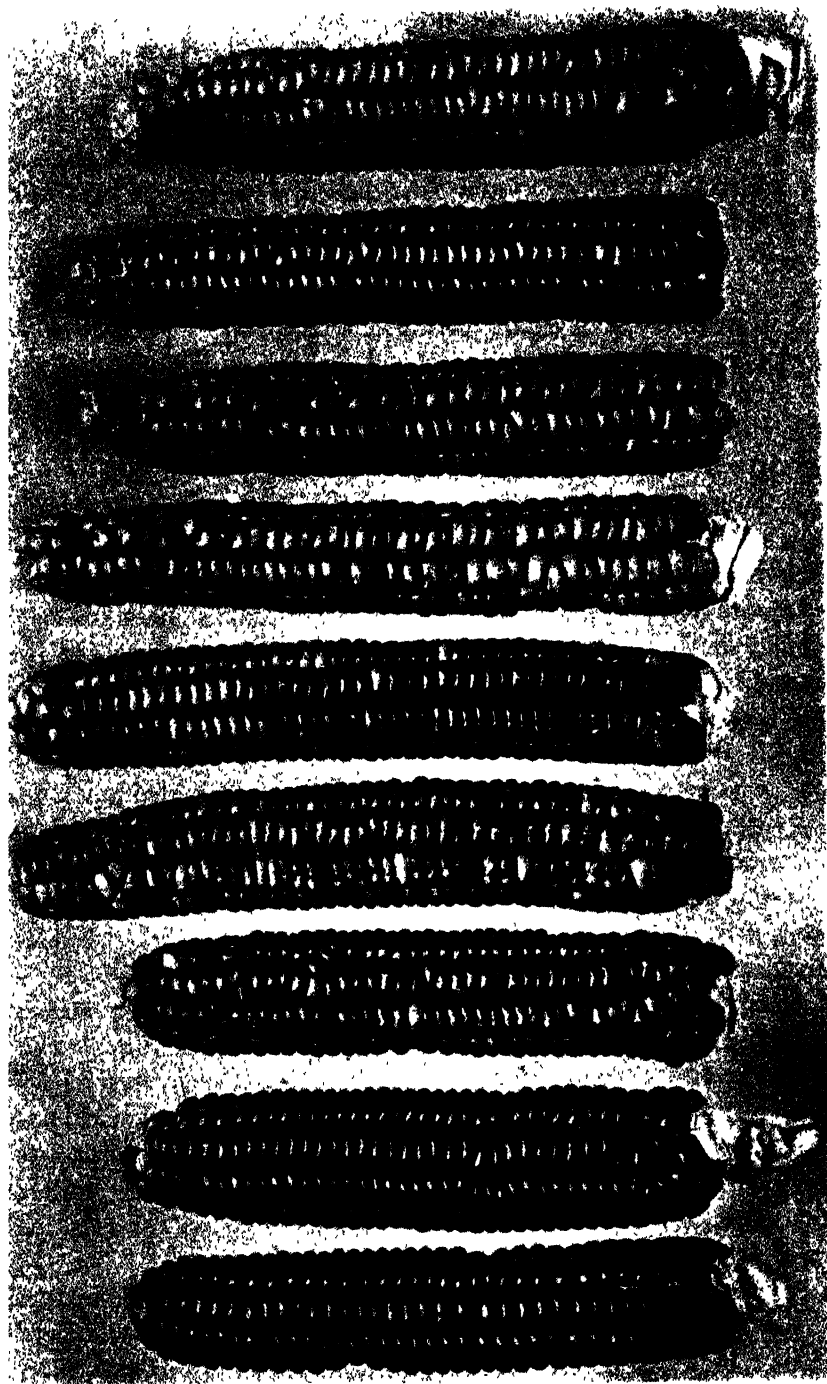


FIGURE 1.—The various types of pericarp color dealt with in this paper. From left to right they represent, respectively, self red, deep mosaic some seeds self, deep mosaic, medium to light mosaic, bud sport, very light mosaic, few deep stripes, pattern color and colorless. (Photograph by HOKRON.)

TABLE 1. Results obtained for pericarp color from self-fertilized ears of Brindle Flint maize

Ear No.	No. gen selfed	Type of parent ear	Progeny classes for color of pericarp								Bud sport	
			Self red	Deep mosaic some seeds self	Deep mosaic	Medium mosaic	Light mosaic	Few seeds striped	Very slight pattern	Colorless	Medium light	Medium few stripes
(69-5)	1	Deep mosaic		20 dark and light mosaic	38 mosaic			20 non-mosaic (pericarp pattern and colorless)				
(69-5)	1	Medium mosaic		74 dark mosaic				13 non-mosaic (pericarp pattern and colorless)				
(69-5)	2	Deep mosaic						23 non-mosaic (pericarp pattern and colorless)				
(69-5)	3	Deep mosaic										
(69-5)	4	Deep mosaic										
(69-5)	5	Medium mosaic										
(69-5)	6	Medium mosaic										
(69-5)	7	Pattern										
(69-5)	8	Pattern										
(69-5)	9	Pattern										
(69-5)	10	Pattern										
(69-5)	11	Pattern										
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(69-5)	194	Pattern										

seemed impossible are placed half way between the two class headings in this table.

While it is possible that some variation may occur, due to a changing ideal as to the value of a particular class, the classification given serves its purpose as it differentiates between heavily striped ears and ears in which the seeds are less heavily splashed with red striations.

The classes self red, deep mosaic some seeds self, and few seeds striped, are of a more distinct type and present little difficulty as regards uniform classification.

Table 1 gives the results obtained from the self-fertilized ears, the progeny of each ear being given separately. Column 1 under Ear No. gives the pedigree of the ears grown, column 2 gives the number of generations that the particular line has been self-fertilized, column 3 gives the type of pericarp of the parental ear while the remaining columns show the range of variation and classification of the progeny of any particular ear.

In a consideration of the results obtained, each pedigree line will be separately discussed.

The progeny for the first two years were not very carefully classified. Beginning with the second generation there is, however, a uniform classification.

The results obtained show a general degree of uniformity for the various types of self-fertilized ears grown. We shall first discuss the families grown from self-fertilized self red pericarp ears.

Family (69-6)-10-6-4 gave a progeny of 35 red ears. Two selections of later generations showed a total progeny of 114 ears all of which had a self red pericarp. The fourth generation selection of family (69-6)-10-1-5 was grown from a self-fertilized self red ear and gave 36 self red ears and 4 in the deep mosaic some seeds self class. As none of the four variegated ears were self-fertilized it was impossible to determine whether they were somatic or germinal variations from the self red type.

One fifth generation and two sixth generation selections gave a total of 123 self red pericarp ears. One third generation family (69-6)-14-3 and three fourth generation lines grown from self-fertilized self red pericarp ears gave a total progeny of 205 self red ears, 26 deep mosaic some seeds self and 7 deep mosaic. One fifth generation family gave a progeny of 54 self red ears.

The sixth and seventh generations of family (69-6)-14-5-6-8-6 gave a total of 146 self red ears and 1 deep mosaic some seeds self ear. In

no case has it been possible to test by breeding experiments the nature of the few deep mosaic ears obtained from self red parentage.

The results given show that the self red ears obtained from variegated parentage tend to give self red progeny. In two families, (69-6)-10-6-4 and (69-6)-10-1-5-1, a total progeny of 233 self red pericarp ears were obtained with no ears in the variegated class.

Two self-fertilized ears of the deep mosaic some seeds self class, (69-6)14-5-6-8 and (69-6)-10-1, behaved as if hybrids between homozygous variegated and pure self red parents, giving a total of 29 self red ears, 45 deep mosaic some seeds self, 6 deep mosaic, 15 medium mosaic, 1 light mosaic, or a total of 67 variegated to 29 self red ears.

This is a ratio per 4 of 2.792 : 1.208. The probable error for this ratio as computed by EAST and HAYES (1911) is ± 0.143 . This is, therefore, a fairly close approximation to a 3 : 1 ratio.

The progeny of self-fertilized deep and medium mosaic ears can be placed in four groups: *Group 1*, in which the progeny ranges from self red ears to ears with a few seeds striped, the proportion of self red ears being about one-third of the total progeny; *Group 2*, in which the progeny show only a few isolated cases of the production of self red ears, the remainder being variegated ears; *Group 3*, in which the range of variation is from self red ears to ears with a very slight pattern; *Group 4*, which gives ears ranging from medium mosaic to the few seeds striped class.

Group 1 is represented by the progeny of (69-6)-5, 4 other selections of later generations of this line, (69-6)-10-6 and (69-6)-14-5-6. The total progeny of these self-fertilized parental ears is as follows: 73 self red ears, 31 deep mosaic some seeds self, 52 deep mosaic, 105 medium mosaic, 28 light mosaic and 38 few seeds striped. This makes a total of 254 variegated to 73 self red ears or a ratio per 4 of 3.107 : 0.893. The deviation from a 3 : 1 ratio is 0.107 and the computed probable error ± 0.065 .

Of the variegated ears 13 percent were placed in the deep mosaic some seeds self class and 20 percent in the deep mosaic class. The variegated ears, obtained from self-fertilized deep mosaic some seeds self parental ears previously mentioned, gave 67 percent of the variegated ears in the deep mosaic some seeds self class and 9 percent in the deep mosaic class. These results show that self-fertilized ears of the deep mosaic some seeds self type give a larger percentage of deep mosaic some seeds self ears than is obtained from self-fertilized deep or medium mosaic ears.

Group 2 consists of family (69-5)-1 and five selections of later gener-

ations. The progeny consisted of the following ears:—1 self red, 1 deep mosaic some seeds self, 19 deep mosaic, 150 medium mosaic, 22 light mosaic, 36 few seeds striped and 1 very slight pattern and 3 either colorless or very slight pattern.

Disregarding the very slight pattern ears, the proportion of self red ears to variegated is in the ratio of 1 to 77.3. It is possible that ear (69-6)-18-8-3 also belongs to this group, although 7 ears were classified as very slight pattern.

Group 3 may be represented by family (69-6)-4 and four selections of later generations. The progeny of these self-fertilized deep and medium mosaic ears consisted of ears as follows:—2 self red, 23 deep mosaic some seeds self, 27 deep mosaic, 116 medium mosaic, 21 light mosaic, 6 few seeds striped, 47 very slight pattern and 23 which were classed as either very slight pattern or colorless.

Considering the doubtful ears as belonging to the very slight pattern class there is a ratio per 4 of very slight pattern to variegated and self red pericarp ears of 1.057:2.943. The deviation from a 1:3 ratio is 0.057 and the probable error ± 0.072 .

Group 4 may be represented by some generations in family (69-5)-9 in which the range of variation of the progeny consists of the three classes medium mosaic, light mosaic and few seeds striped.

Family (69-5)-9 and later generations consist of a progeny of 181 few seeds striped ears, 531 light mosaic ears and 112 medium mosaic ears. As no ears of a higher grade than medium mosaic or a lower grade than few seeds striped were obtained it will be noted that this family is homozygous for variegation.

The question at once suggests itself: Do self-fertilized ears of the few seeds striped class give a larger proportion of progeny of this grade than self-fertilized medium mosaic ears? As a means of answering this question table 2 has been prepared from the data given in table 1. The percentage of ears of the different grades, medium mosaic, light mosaic and few seeds striped, is given in the table. In discussing these results it should be stated that there is no sharp border line between these different classes. The class few seeds striped is, however, of a more definite type than the other two classes.

A careful study of table 2 shows that self-fertilized medium or light mosaic ears give a smaller percentage of few seeds striped progeny than is obtained from self-fertilized few seeds striped ears. As neither grade, medium mosaic nor few seeds striped, breeds true, and as no definite

TABLE 2

Selection experiments within family (69-5)-9 which bred true for a range of variation from medium mosaic ears to ears with a few seeds striped.

Parentage	Generation	Type of parent ear	Progeny		
			Percent of medium mosaic ears	Percent of light mosaic ears	Percent of few seeds striped ears
69-5-9-9-5	4	Light mosaic	21	71	8
69-5-9-9-6		Light mosaic	10	83	7
69-5-9-9-2		Light mosaic	0	80	20
69-5-9-9-1		Few seeds striped	2	69	29
69-5-9-9-2-5	5	Medium to light	66	9	25
69-5-9-9-2-2		Few seeds striped	19	25	56
69-5-9-9-1-5		Medium mosaic	18	82	—
69-5-9-9-1-7		Few stripes	27	13	60
69-5-9-9-1-5-5	6	Medium mosaic	44	48	8
69-5-9-9-2-5-10		Medium mosaic	4	90	6
69-5-9-9-2-5-14		Light mosaic	11	89	0
69-5-9-9-2-5-4		Light mosaic	—	88	12
69-5-9-9-2-2-11		Few stripes	—	70	21
69-5-9-9-2-5-10-1	7	Medium mosaic	8	84	8
69-5-9-9-2-5-14-3		Medium mosaic	6	61	33

ratios are obtained, these results do not appear to be of the usual Mendelian type of segregation.

Self-fertilized ears of the very slight pattern type are represented by ear No. (69-6)-4-2-6-8-2, one selection of a later generation, ear No. (69-6)-4-1 and three selections of later generations. In one case ear No. (69-6)-4-2-6-8-2-7 a considerable percentage of variegated ears were obtained. These may possibly be due to accidental causes. The other self-fertilized ears gave a total progeny of 240 ears of which 239 were of the very slight pattern type, while 1 showed a single deep red stripe on one seed.

It seems reasonable to conclude, therefore, that ears can be isolated which are homozygous for slight pattern. There is, however, the possibility of a gradual cumulative effect and thus the production of an occasional ear of a higher grade of variegation.

Family (69-5)-8-3 and six selections of later generations consisted of self-fertilized colorless pericarp ears. Four ears of the very slight pattern type, 7 of the light mosaic and few seeds striped class, and 263

colorless pericarp ears were obtained. As none of the variegated ears were selfed it is impossible to say how they would breed.

RESULTS OF SELECTION EXPERIMENTS

1. Selection experiments with a mosaic pericarp pattern color of corn have isolated the following types which breed comparatively true:

- (a) A self red pericarp;
- (b) Pure for variegation but giving a range of variability from ears with only a few seeds with deep red stripes to ears in which nearly all seeds are quite heavily covered with red striations;
- (c) A type with a very slight pattern color which under the microscope appears to be due to the presence of a faint color in some of the pericarp cells;
- (d) An uncolored pericarp race.

2. Selection within type (b) which breeds true for variegation has not succeeded in isolating strains which breed true for amount of variegation. Extreme minus types within this strain tend to give a progeny containing more ears of the minus type than are obtained from extreme plus types.

3. Heavily striated self-fertilized ears have proven to be heterozygous, giving a progeny which exhibits segregation for one factor difference.

4. The very deeply variegated heterozygous self-fertilized ears give a progeny in which a greater proportion of the variegated segregates are deeply variegated than is obtained in the progeny of less deeply variegated self-fertilized heterozygous ears.

CROSSES BETWEEN SELECTED TYPES

After isolating several comparatively pure types by selection it was decided to determine their mode of inheritance and relationship to each other by crosses between these various types. For convenience the various crosses will be considered as families and discussed separately.

Family 1. Reciprocal crosses between the self red pericarp type and the homozygous variegated type which exhibited a range of variation from medium mosaic ears to few seeds striped ears

The results from this cross are presented in table 3. Three F_1 crosses are given in the table, reciprocal crosses giving like results. A total of 15 deep mosaic and 84 medium mosaic ears were obtained in the F_1 generation. Five F_1 self-fertilized ears gave the same sort of segregation in F_2 . A total progeny was obtained of 98 self red ears, 89 deep

TABLE 3
First and second generation of cross between self red selection (69-6)-10-6-4 and (69-5)-9-9, a selection which breeds true for a range of variation between medium mosaic ears and ears with a few seeds with deep red stripes.
Back-crosses of F_1 with the parental lines.

Cross	Generation	Progeny classes				
		Self red	Deep mosaic	Medium mosaic	Light mosaic	Few seeds striped
(69-6)-10-6-4-1-10 × (69-5)-9-9-2-5-4 = 1D	F ₁		2	55		
(69-6)-10-6-4-5-3 × (69-5)-9-9-1-5-2 = 3D	F ₁		12	13		
(69-5)-9-9-2-2-6 × (69-6)-10-6-4-5-7 = 2D	F ₁		1	16		
1 D - 2	F ₂	24	26	23	10	2
1 D - 5	F ₂	27	13	25		1
2 D - 6	F ₂	11	19	21	18	6
2 D - 5	F ₂	17	16	34	11	5
3 D - 6	F ₂	19	15	48	21	7
2 D - 1 × (69-5)-9-9-2-5-14-1	F ₁ × variegated parent		17	42 ¹	33	9
2 D - 1 × (69-6)-10-6-4-5-7	F ₁ × self red parent	42	18	27		1

¹ a = ear bud sport one-half medium mosaic one-half few stripes.

mosaic ears, 151 medium mosaic ears, 69 light mosaic ears and 21 few seeds striped ears. This is a ratio per 4 for variegated to self red of 3.084 : 0.916. The probable error in this case is ± 0.056 .

One F_1 generation ear was pollinated by the variegated parent and gave a progeny of 17 deep mosaic, 41 medium mosaic, 33 light mosaic, 9 few seeds striped, and 1 bud sport, a part of the ear being medium mosaic, the other part belonging to the few seeds striped type.

The back-cross of the F_1 with the self red parent gave 42 self red ears, 18 deep mosaic ears and 27 medium mosaic ears.

The results obtained from the F_2 generation and the crosses of F_1 with the parental types, respectively, show that one main factor difference is involved. If we consider these factors as M and S respectively, we may conclude that M and S are allelomorphs or according to MORGAN's chromosome hypothesis, located in corresponding loci of homologous chromosomes.

Family 2. First and second generation crosses of homozygous self red pericarp and pattern selections

The same self red races were used as for the cross between self red and homozygous variegated described in the previous family. The F_1 generation cross of the self red with the pattern selection consisted of self red ears and in F_2 109 self red ears, 39 pattern ears and 1 ear with one deep red stripe on one seed was obtained. This is a clear indication of a 3 : 1 ratio.

Comparing these results with family 1 shows a complete dominance of the self red pericarp in one cross and an intermediate condition in the other cross. There is a greater difference in character between the self red and pattern types than for the self red and variegated selections. Complete dominance was obtained in the cross in which the parental varieties differed most widely.

TABLE 4

First and second generation of cross between selection (69-6)-4-1-6-2-7 and (69-6)-4-1-6-8-3, which breed true for pattern color, and (69-10)-1-5-1-2 and (69-10)-6-4-5-1, selections which breed true for self red pericarp.

Cross	Generation	Progeny classes	
		Self red	Pattern
(69-6)-4-1-6-2-7 \times (69-10)-1-5-1-2 = 1 B	F_1	58	
(69-6)-4-1-6-8-3 \times (69-10)-6-4-5-1 = 2 B	F_1	All self	
1 B - 8	F_2	53	*21 ²
2 B - 1	F_2	56	19

*2a = Deep red stripe on one ear.

Family 3. First and second generations of the cross between the pattern selection and the variegated type

The parental types are the recessive selections of the crosses given in families 1 and 2. *MM* represents the selection which proved to be homozygous for the variegated character. Table 1 shows a total progeny of 324 ears obtained in family (69-5)-9 all of which were of the variegated type. *PP* represents the pattern type, (69-6)-4-1-6, which bred true to the pattern condition. These two selections when crossed with the self red pericarp type showed the ordinary Mendelian expectation in F_2 for one factor difference.

The results obtained for the cross between variegated and pattern selections are presented in table 5.

The F_1 generation consisted of 143 variegated ears and 1 ear of the pattern type. Of the variegated ears 5 were classed as deep mosaic which is a higher grade than was obtained in the homozygous variegated parent and 4 were classed as bud sports. As no bud sports appear in either of the homozygous parental varieties, it would seem as if crossing has in some way produced a condition of instability. This instability is also shown by the increased variability obtained in F_1 from crossing apparently homozygous types.

Nine self-fertilized F_1 ears were grown in F_2 . Three of these ears were of the bud sport type, while of the other six 5 were classed as light mosaic and one as medium mosaic. The three ears classed as bud sports gave a total progeny of 188 ears, 10 of these being bud sports. The "non-sport" ears gave a total progeny of 445 ears, 11 of which were bud sports. The ratio of bud sport ears from self-fertilized bud sport parentage is 1 bud sport to 18.8 normal. When normal ears were planted 1 of the bud sport type was obtained to 40.4 ears of the normal type.

The F_2 generation exhibits a greater variability than the F_1 . Nine F_1 self-fertilized ears gave a total progeny in F_2 of 12 self red ears, 420 variegated ears ranging from deep mosaic some seeds self to ears with only a few seeds striped with deep red, 21 which exhibited sharp segregation of characters on the ear, a part of the ear being of one type, the remainder being of another type and 201 ears of the pattern type.

This is a total of 201 pattern ears to 453 of the variegated and self red classes or a ratio per 4 of pattern ears to other sorts of 1.229:2.771

TABLE 5

First and second generation of cross between selection (69-6)-4-1-6 which breeds true for the pattern pericarp, with selection (69-5)-9-9-2 which breeds true for a range of variation from medium mosaic ears to ears with a few seeds striped.

Cross	Generation	Type of parent ear	Progeny classes						Bud sports							
			Self red	Deep mosaic	Deep mosaic self	Deep-mosaic	Medium mosaic	Light mosaic	Few seeds striped	Pattern	Medium—light	Medium—few seeds striped	Deep—light	Light—few seeds striped	Medium—pattern	Light—pattern
(69-6)-4-1-6-2-12 × (69-5)-9-9-2-5-6 = 4 A	F ₁			5		5	21	3	1				1			
(69-6)-4-1-6-8-1 × (69-5)-9-9-2-2-4 = 3 A							10	20	2	1			1			
(69-6)-4-1-6-2-11 × (69-5)-9-9-2-2-10 = 2 A							14	23	10		1					
(69-6)-4-1-6-8-2 × (69-5)-9-9-2-2-1 = 1 A	F ₁						10	15	5		1					
Total				5		5	55	61	18	1	2		2			
1 A—1	F ₂	Bud sport medium —few stripes														
1 A—5		Bud sport	1	3		3	7	12	4	16		1		2		
1 A—2		Light mosaic		3		3	4	14	8	8		3		2		
1 A—3		Light mosaic		3		3	13	20	12	17				2		
2 A—5		Light mosaic	4	1		5	8	24	14	22		4				
3 A—3		Light mosaic	7	3		5	17	20	10	28		1		1		
3 A—6		Light mosaic				4	18	20	9	24		1				
4 A—2		Light mosaic				4	14	25	14	33		1				
4 A—2		Bud sport		3		3	13	28	23	37		1		1	2	
4 A—3		Medium mosaic					8	27	4	16						
Total	F ₂		12	4	26	102	190	98	201		11		4	2	4	

Family 4. First and second generation of cross between the homozygous variegated and colorless selections

The results of this cross are presented in table 6. The F_1 generation consisted of 41 variegated ears. In F_2 103 variegated, 17 pattern, and 28 colorless pericarp ears were obtained. One of the variegated ears was of a higher grade than the F_1 or variegated pattern type. The nature of these 17 pattern ears could only be determined by breeding test, which was impossible, as none of these ears happened to be selfed.

As only a single cross between variegated and colorless has been studied, it does not seem wise to make an extended discussion of these results. The deviations from simple Mendelian expectations might be explained by supposing the variegated factor M to change to a factor for self color S or to the pattern factor P . It is equally possible that these results might be explained by accidental chance pollination.

RESULTS OF CROSSING HOMOZYGOUS TYPES

1. The cross between the self red selection SS and the homozygous variegated type MM gave an intermediate F_1 which consisted of ears which were more deeply striated than the homozygous variegated race. The F_2 generation grown from self-fertilized F_1 ears showed a segregation of self red, F_1 , and homozygous types, as expected for one unit-factor difference. Back-crosses of the F_1 with the parental strains gave parental and F_1 types in a 1 : 1 ratio.

2. The cross between the self red selection SS and the pattern selection PP showed a dominance of the self red type in F_1 and in F_2 a segregation of self red and pattern types in a 3 : 1 ratio.

3. The cross between the homozygous variegated selection MM and the pattern selection PP gave an increase of variability in F_1 which was shown by ears of a higher grade for variegation than the parental variegated race and by the production of a considerable proportion of bud sport ears. In F_2 some self red ears were obtained. The proportion of pattern ears to other grades was 1 to 2.3.

4. The cross between the homozygous variegated race, MM , and the colorless race, CC , gave F_1 ears of the variegated type and a segregation in F_2 . One ear of a higher grade than the F_1 and a number of ears of the pattern type were obtained as well as a considerable number of ears of the two parental types.

TABLE 6
First and second generation of cross between colorless pericarp selection (69-5)-8-3-5-2-3 and light mosaic selection (69-5)-9-9-2-5-5.

Cross	Gen.	Progeny classes					
		Deep mosaic few seeds self	Deep mosaic	Medium mosaic	Light mosaic	Few stripes	Pattern
(69-5)-8-3-5-2-3 × (69-5)-8-8-2-5-5 = C C—6 C—7	F ₁			13	25	3	
	F ₂	1		13	35	7	11
	F ₂			6	35	6	6
							14
							14

DISCUSSION AND INTERPRETATION OF RESULTS

The results presented in the experiments are of two sorts:

1. Those which show the usual type of Mendelian inheritance, i.e., dominance, recessiveness, and segregation with definite ratios.
2. Results which are not easily explained by the hypothesis of absolute purity of fundamental factors of inheritance.

The use of several main factors is helpful in an explanation of the Mendelian results obtained. The letters *S* and *M* respectively denote factors for self color and variegation. The letter *P* may be used to denote the very slight pericarp pattern factor which in the absence of *M* or *S* produces a slight pattern color. This appears to be a true pattern factor as a portion of the cells of the pericarp of a homozygous very slight pattern race show a slight color while other cells appear to contain no coloring matter.

Selection experiments served to isolate races which bred comparatively true for the following pericarp characters: Self red, *SS*, homozygous variegated, *MM*, very slight pattern, *PP*, and colorless, *CC*. The crosses between self red, *SS*, very slight pattern, *PP*, and self red with homozygous variegated, *MM*, showed that these factors are distinct in inheritance. The ratio obtained for the F_2 of the self red—pattern cross was 3:1 and for the self red—variegated cross was 1:2:1. The fact that no new types were produced by these crosses would indicate that *P*, *M* and *S* were multiple allelomorphs. It is impossible to say which is the normal condition from which the other types were produced.

The cross between *MM* and *PP* gave results of a different nature. Before discussing these results it may be well to discuss the evidence for purity of the parental types used. Before making the cross the parental varieties were self-pollinated for several generations. The progeny of the self-fertilized ears of the slight pattern type, *PP*, consisted of 219 ears of the pattern type and 1 ear with a single deep red stripe on one seed. As this ear was open-pollinated it was impossible to determine whether or not this was a germinal variation. The variegated family (69-5)-9 and later self-fertilized generations showed a total of 824 ears all of which were of the variegated type. No ears were produced which did not have a deep red stripe on at least one seed and no ears which were of a higher grade than the medium mosaic class. Within this family self-fertilized medium and light mosaic ears tended, however, to give a larger proportion of ears in the medium and light mosaic class than self-fertilized few stripe ears. Seeds of 6 self-fertilized medium

mosaic ears which were grown in four successive generations did not materially decrease the range of variegation. Somewhat similar results were obtained in the progeny of 5 self-fertilized light mosaic ears and in the progeny of 3 self-fertilized few stripe ears. There is also no marked uniformity of results for the different types of self-fertilized ears and no indication of definite segregation. These results could be brought into line with EMERSON'S by supposing a separate factor for medium variegation M_m which is allelomorphic to a factor for light variegation M_l and by further supposition of frequent germinal variations of M_l to M_m and *vice versa*.

As this family breeds true for variegation, we may conclude that it is homozygous for a factor for variegation, or MM (= "mosaic"). The hypothesis of slight germinal variations for the variegated factor seems to be a simpler explanation of the results obtained than the supposition of a definite change from M_l to M_m .

The cross between the variegated type and the very slight pattern type showed a dominance in F_1 of the variegated race. There was also an increase in variability in F_1 and ears of a higher grade of variegation were obtained than in the progeny of the homozygous variegated parent. Table 1 shows that no bud sport ears were obtained in the homozygous parental selections. The F_1 generation of the cross, however, showed 4 ears of the bud sport type in a total of 144 ears. This is between 2 and 3 percent.

The F_2 generation of this cross gave a little over 36 percent of the progeny in the pattern class, 58 percent of the variegated type, 2 percent bud sports and 4 percent self red pericarp ears. As four different crosses between the pattern and variegated races were studied and as results were of the same nature for each cross, they seem fairly dependable.

If M and P were not allelomorphs some F_2 combinations would lack both M and P and presumably lack color in the pericarp. As no such ears were obtained and as there is considerable evidence which seems to show that M and P are respectively allelomorphic to the factor for self color, S , there seems to be sufficient reason for concluding that M and P are allelomorphs.

We may then suppose that the union of M and P in F_1 causes some sort of contamination which produces a condition of instability. In some cases the M factor may change to the self red form, S . The instability of this zygotic combination MP is further shown by the pro-

duction of a considerable proportion of bud sport ears. As few sports (none having been observed) are produced in the self-fertilized parental forms, *MM* and *PP*, one might conclude that certain heterozygous combinations produce germinal instability which exhibits itself either as imperfect segregation, gametic contamination or sporophytic variation.

SUMMARY

Variegated or pattern characters have generally been considered to be of unstable nature. Self-fertilization and selection within a red mosaic pericarp pattern color of maize isolated several types which bred relatively true. The types for pericarp color were self red, variegated, pattern and colorless. Evidence is given which shows that the self red, pattern and colorless selections are homozygous for these characters. The variegated selection proved to be homozygous for the mosaic character and gave a range from ears in which nearly all seeds were heavily striated to ears in which only a few seeds showed red stripes. Extreme plus ears tended to produce a progeny with more ears of the plus type than was obtained in the progeny of few stripe ears. The range of variation, however, was not affected by such selection. These results are explained by the hypothesis of slight germinal variations.

The relation of these various pericarp characters was then studied by making crosses between the various homozygous types. The cross between self red and variegated gave an F_1 with a more intense variegation than the variegated parent and a ratio of 1 : 2 : 1 in F_2 . The self red—pattern cross gave self red ears in F_1 and a ratio of 3 self red to 1 pattern in F_2 . The pattern—variegated cross gave an F_1 with a greater range of variation than either parent. Nearly all ears had a variegated pericarp, several being of a higher degree than the variegated parent. The unstable nature of this cross was further shown by the production of a considerable percentage of bud sport ears. A few self red ears were obtained in F_2 , many variegated ears, nearly half as many pattern ears, as well as a number of bud sport ears. The suggestion is made that certain combinations produce germinal instability. The conclusion is then reached that the factors for self red, variegated, pattern and colorless pericarp form a series of multiple allelomorphs.

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SUPPLEMENTARY DETERMINATIONS OF THE RELATIONSHIP BETWEEN THE NUMBER OF OVULES PER POD AND FERTILITY IN PHASEOLUS¹

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INTRODUCTION

One of the phases of a study of the physiology of seed production which has been under way for the past ten years has been the investigation of the relationship between the number of ovules laid down per pod and the capacity of the pod for maturing these ovules into seeds.

In adequately large series of observations, the value of r_{os} , the correlation between the number of ovules formed, o , and the number of seeds developing, s , per pod, has always been found to be positive. Furthermore, the relationship in *Phaseolus*, and in some other legumes which have been thoroughly investigated, may be *fairly* satisfactorily represented by the slope of a straight line. In other words, the mean number of seeds matured per pod increases at practically a uniform rate from the lowest to the highest number of ovules formed.

Such a relationship would be expected if the failure of individual ovules to develop into mature seeds were due to purely random causes. Its existence cannot, however, be taken to indicate that the failure of the ovules to develop into seeds is due solely to such causes. The correlation constant r_{os} is of descriptive value only. It may differ significantly from species to species or from environment to environment. Thus the average of the correlation between number of ovules and number of seeds in *Staphylea* has been shown (HARRIS 1912) to be .0282 for a lot of 20 shrubs from which collections were made in 1906 and .0658 in a series of 16 determinations from individual shrubs in 1907. For *Cercis* (HARRIS 1914) the correlations are .648 for a series from Meramec Highlands, Mo., .603 for a series from the vicinity of Lawrence, Kansas, and .455 for materials from the neighborhood of Sharpsburg, Ohio. For *Sanguinaria* (HARRIS 1910) the values are over .800.

¹ Studies on the correlation between morphological and physiological characters. IV.

Many other constants from published and unpublished data might be given, but since they merely serve to illustrate the variability of the correlation between the actual number of ovules laid down and the actual number of seeds developing, further examples are superfluous.

But what is needed in physiological investigations is a measure of the relationship between the number of ovules per pod and the capacity of the pod for maturing these ovules into seeds. This need was first realized and met in 1909, when it was shown by Professor PEARSON and myself (HARRIS 1909) that the relationship between the number of ovules per pod and its capacity for maturing its ovules into seeds may be expressed in terms of the correlation between the number of ovules and the deviation of the number of seeds matured per pod from the probable value, that is from the number which would be expected if it were determined solely by the relative proportion of the ovules which developed into seeds in the population at large, i. e., by $p = \bar{s}/\bar{o}$, where the bars denote population means, and not at all by other factors associated with number of ovules per pod. Three years ago the results of the analysis of the first extensive series of data, comprising countings of over 160,000 pods belonging to 53 series of experimentally grown plants representing six varieties of garden beans, were discussed (HARRIS 1913). Since that time numerous data for an arborescent legume, *Cercis Canadensis*, have also been treated. In a first paper (HARRIS 1914 a), the findings for large samples of pods collected from many trees were set forth. In a second memoir (HARRIS 1914 b), the same data were treated for individual trees. It seems unnecessary to do more in the way of general discussion of the subject than to refer to these publications.

MATERIAL AND METHODS

The data upon which the present discussion is based are those of a preceding paper (HARRIS 1917). The method of determining correlation between the number of ovules formed and number of seeds developing, is the usual one.

The values of the correlation between the number of ovules per pod and the deviation of the number of seeds per pod from its probable value has been computed from the usual formula

$$r_{os} = \frac{r_{os} - v_o/v_s}{\sqrt{1 - r_{os}^2 + (r_{os} - v_o/v_s)^2}}$$

where v_o and v_s are the coefficients of variation, $100 \sigma_o/\bar{o}$, $100 \sigma_s/\bar{s}$, the

sigmas denoting standard deviations and the bars indicating population means.

PRESENTATION OF DATA

In the accompanying table the key letters for the 16 cultures are followed by the number of pods upon which the determinations are based.

Series	N	r_{os} and Er_{os}	r_{oz} and Er_{oz}	r_{oz}/Er_{oz}
HHT	3722	.418 \pm .009	-.040 \pm .011	3.64
HHHT	7429	.382 \pm .007	-.083 \pm .008	10.38
HDT	1600	.382 \pm .014	-.094 \pm .017	5.53
HDDT	6408	.362 \pm .007	-.096 \pm .008	12.00
DDT	1151	.381 \pm .017	-.055 \pm .020	2.75
DDDT	3501	.368 \pm .010	-.078 \pm .011	7.09
DHT	2516	.331 \pm .012	-.118 \pm .013	9.08
DHHT	3412	.334 \pm .010	-.126 \pm .011	11.45
USHT	3772	.294 \pm .010	-.072 \pm .011	6.55
USHHT	3087	.276 \pm .011	-.087 \pm .012	7.25
USDT	2601	.260 \pm .012	-.112 \pm .013	8.62
USDDT	4355	.282 \pm .009	-.095 \pm .010	9.50
FSHT	3127	.249 \pm .011	-.098 \pm .012	8.17
FSHHT	3700	.227 \pm .011	-.128 \pm .011	11.64
FSDT	2531	.294 \pm .012	-.065 \pm .013	5.00
FSDDT	3786	.274 \pm .010	-.109 \pm .011	9.91

The third column gives the correlation between the actual number of ovules and the actual number of seeds per pod. The fourth column contains the results for the correlation between the number of ovules per pod and the deviation of the number of seeds from their probable value on the assumption of the absence of any relationship between ovule number and capacity for seed production. The ratios of these constants to their probable errors—measures of their statistical trustworthiness—appear in the final column.

The correlation between the number of ovules formed and the number of seeds developing is positive throughout, with an average of $.3196 \pm .0094$ and a standard deviation of $.0556 \pm .0066$ as compared with a mean correlation of $.3964 \pm .0092$ and a variability in correlation of $.0998 \pm .0065$ in the first series. Thus the mean correlation in the first series is $.0768 \pm .0132$ higher than in the second, but it must be noted (a) that seven varieties are represented in the first series as compared with four in the second, and (b) that the environmental

conditions under which the two lots were grown were very different. The variability in correlation is $.0442 \pm .0092$ higher in the first than in the present series of determinations, but this may also be attributed largely if not entirely to greater heterogeneity in varietal composition and in environmental conditions.

Turn now to the values of r_{os} , the coefficient measuring the relationship between the number of ovules per pod and the capacity of the pod for maturing its ovules into seeds. The constants appear in the fourth column of the table. A measure of their statistical significance, the ratio of the correlation coefficients to their probable errors, is given in the final column of the table. The sign and the magnitude of the constants is also shown graphically in diagram 1, which contains the first 53 as well as the present series. Here the magnitudes of the coefficients, serially arranged, are shown by the length of the lines extending above

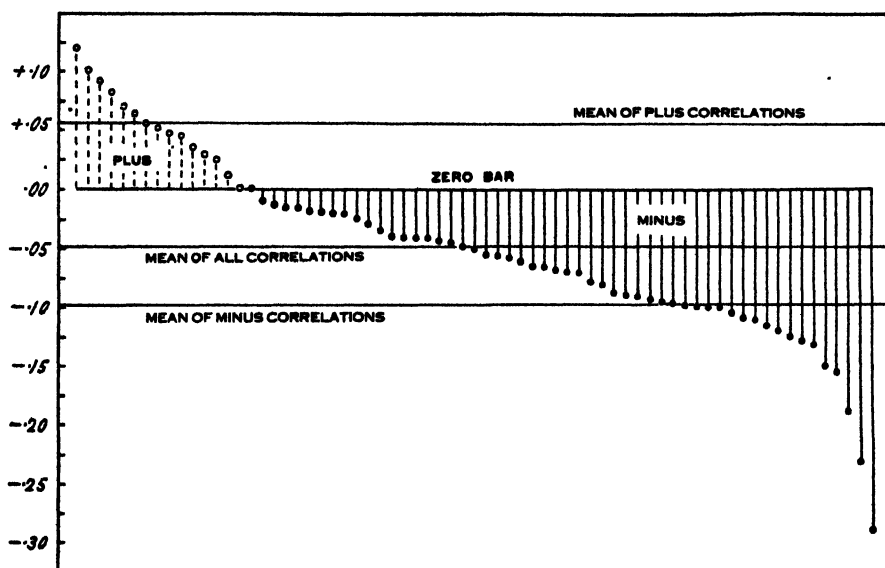


DIAGRAM 1.—Distribution of correlations between number of ovules per pod and the deviation of the numbers of seeds per pod from their probable value.

and below the zero bar for the positive and negative coefficients respectively.

The new series of determinations differs conspicuously from that of the first paper on *Phaseolus* in that the measurements of the present series are negative throughout. In the first series, 38 were negative and 15 positive in sign.

If the results of the two sets of determinations be combined,² it is to be noted that there are 54 negative as compared with 15 positive correlations. This is a deviation from equality (which should be found if there were no biological factors tending to bring about a definite correlation) of

$$(54-34.5) \text{ or } (15-34.5) \pm .67449 \sqrt{69 \times .5 \times .5} = 19.5 \pm 2.80$$

The deviation is over 6.9 times as large as its probable error, and so almost certainly significant.

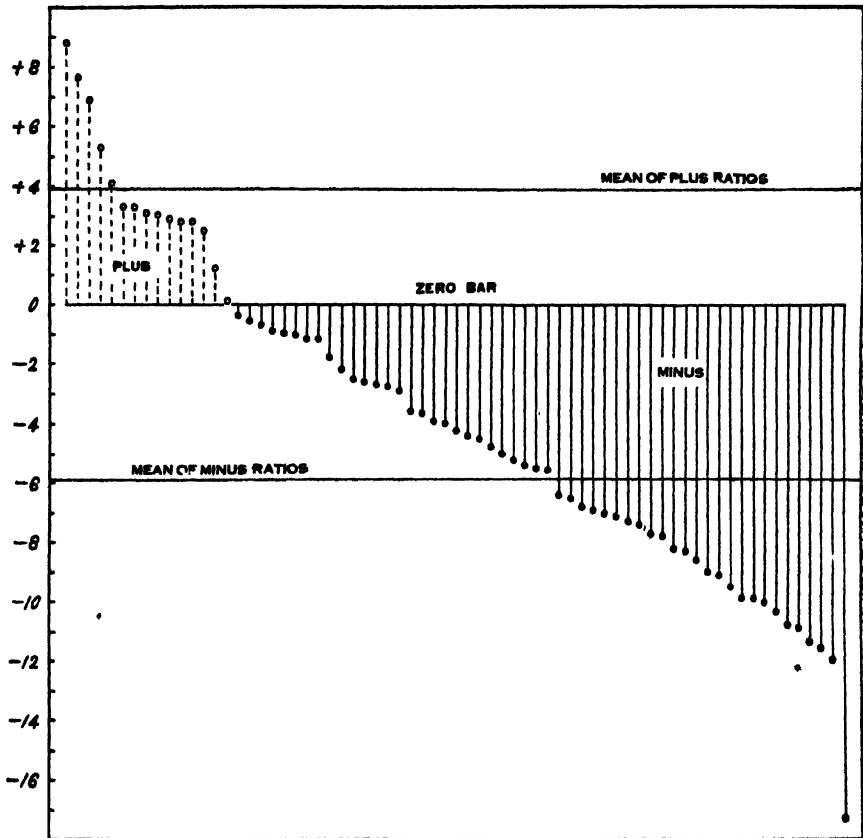


DIAGRAM 2.—Distribution of the ratios of the correlations between the number of ovules per pod and the deviation of the number of seeds per pod from their probable value to the probable errors of these correlations.

² While, as emphasized above, the second series of determinations is technically decidedly the better of the two, it does not represent the range of environmental conditions found in the first. That such conditions may influence the relationship here under consideration is perhaps indicated by the differences demonstrated in an earlier paper, for *Cercis* from Missouri, Ohio and Kansas localities. To avoid all possible criticism as to the selection of data it has seemed wise to consider the two series, both individually and in combination.

Thus if conclusions be based upon the nature of the relationship as indicated by their signs, and without regard to the intensity or statistical trustworthiness of the individual constants, there can be no question concerning the existence of a negative correlation between number of ovules per pod and capacity for seed production.

This conclusion receives substantiation of the most convincing sort from an examination of the relation of the individual constants to their probable errors.

These are shown in the final column of the table of constants and are represented graphically for the 69 determinations available from the first and second series in diagram 2. This is constructed in the same manner as diagram 1, except that the length of the bars indicates the magnitude of the coefficients in relation to their probable errors, i. e., the ratio of the constants to their probable errors.

Of the 69 determinations, 57 are at least 2.5 times as large as their probable errors. Of these, 44 are negative as compared with 13 which are positive in sign. Of the 40 constants which are over 4 times as large as their probable errors, 35 are negative as compared with only 5 which are positive in sign. Finally, there are 24 values which are over 7 times as large as their probable errors. Of these, 22 are negative as compared with 2 which are positive in sign.

Thus, judged by the measures of the statistical significance of the individual constants, there can be no possible question that the negative coefficients are far more trustworthy than are the positive ones. The average ratio of the 54 negative correlations to their probable errors is 5.97 as compared with 3.87 for the positive.

Consider now the actual magnitudes of the correlations.

The constants for correlations (r_{oz}) in the two series are:

	Mean	Standard deviation
First series	$-.0365 \pm .0075$	$.0811 \pm .0053$
Second series	$-.0910 \pm .0040$	$.0242 \pm .0028$
Difference	$.0545 \pm .0085$	$.0569 \pm .0060$

Thus the mean value of the correlation is numerically higher and the variability of the correlation significantly less in the second series of determinations. The difference in the means is $.0545 \pm .0085$, or over 6.4 times as large as its probable error. The standard deviation for the second group of constants is less than a third of that found for the first lot. The actual difference is $.0569 \pm .0060$, or an amount over 9.4 times as large as its probable error.

This is precisely the result which would be expected if perfection of the experimental and observational conditions resulted in the detection in every instance of a relationship hitherto often obscured by uncontrolled factors. The second series is unquestionably the better of the two. It evidences much more strongly for the existence of a negative relationship between the number of ovules formed and the capacity of the pod for maturing its ovules into seeds.

The constants for the 69 determinations resulting from a combination of the earlier and the present series are:

$$\begin{array}{ll} \text{Mean} & -.0491 \pm .0061 \\ \text{Standard deviation} & .0786 \pm .0043 \end{array}$$

Variety		Number of series	Mean r_{oz}	Mean r_{oz}/Er_{oz}
Golden Wax	Plus correlation	—	—	—
" "	Minus correlation	3	-.081	-4.20
" "	All correlation	3	-.081	—
Black Wax	Plus correlation	—	—	—
" "	Minus correlation	2	-.262	-8.49
" "	All correlation	2	-.262	—
Burpees Stringless	Plus correlation	—	—	—
" "	Minus correlation	8	-.055	-5.46
" "	All correlation	8	-.055	—
Navy H	Plus correlation	6	+.074	+5.48
" "	Minus correlation	7	-.061	-6.82
" "	All correlation	13	+.001	—
Navy D	Plus correlation	6	+.050	+3.28
" "	Minus correlation	7	-.070	-5.70
" "	All correlation	13	-.015	—
Ne Plus Ultra	Plus correlation	1	+.071	+2.78
" " "	Minus correlation	14	-.077	-5.56
" " "	All correlation	15	-.067	—
White Flageolet	Plus correlation	2	+.014	+1.35
" "	Minus correlation	13	-.079	-6.41
" "	All correlation	15	-.066	—

The mean value differs from 0 by over 8 times the probable error of the determination. There can, therefore, be no question concerning its significance.

If the determinations be divided into two groups, positive and negative, the averages are:

$$\begin{array}{ll} \text{Positive constants} & +.0565 \\ \text{Negative constants} & -.0785 \end{array}$$

The averages for each variety are shown in the accompanying table. Without exception there are more negative than positive correlations in each variety. Without exception the negative correlations show a higher degree of statistical trustworthiness in each variety than do the positive correlations. With the single exception of the Navy H series, in which the mean correlation is positive by an insignificant amount, the mean correlation is negative in sign in each variety.

Thus while the number of determinations for each variety must of necessity be small, the results for the individual strains substantiate in a most striking manner the conclusions drawn from the data as a whole.

DISCUSSION OF RESULTS

The present paper is devoted to the problem of the relationship between the number of ovules formed per pod and the capacity of the pod for maturing these ovules into seeds.

The relationship is measured in terms of the correlation between the number of ovules per pod and the deviation of the number of seeds per pod from the probable number on the assumption that the chances of an individual ovule developing into a seed are quite independent of the number of ovules in the pod in which it is produced. Sixteen new series of data for Phaseolus, comprising countings of number of ovules formed and number of seeds developing per pod in 56698 pods, are presented, and the constants deduced from them compared with those from 53 series comprising 166130 pods published in an earlier paper.

These lead to the conclusion that there is a negative relationship between number of ovules formed per pod and capacity for maturing these ovules into seeds, i. e., that pods with larger numbers of ovules show a relatively lower capacity for maturing their ovules into seeds.

Either of these series taken independently may be considered as establishing the conclusion drawn. The second, however, not merely substantiates the first, but indicates that the law holds even more rigorously than appeared from the first series of data. In the first 53 determinations, only 15 out of 53 constants were exceptions to the rule. In the second series, the results are consistent throughout. In the first series, the mean value of r_{oe} , which should be zero if there were no relationship between number of ovules per pod and capacity for maturing seeds, is negative in sign and about five times as large as its probable error. In the second series, it is negative in sign and over twenty times as large as its probable error. In the first series of determinations, 41 of the 53

constants are at least 2.5 times as large as their probable errors. In the second series each of the 16 constants is at least 2.5 times as large as its probable error, and many are several times as large as their probable errors.

As biological facts, the results presented here seem soundly established, so far as the species in question is concerned, and represent, therefore, one further step in the analysis of the problem of fertility and fecundity in plants. The physiological interpretation of the results is quite another matter. Anyone venturing to suggest explanations must bear in mind that the problem is one involving many factors and surrounded by many difficulties which need not be discussed here. It is reasonable to believe that these difficulties like those which have surrounded the carrying of the investigation up to the present point, will ultimately be overcome by the application of biometric formulae to appropriately collected masses of quantitative data.

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SEVERAL COLOR "MUTATIONS" IN MICE OF THE GENUS PEROMYSCUS

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In the course of breeding experiments conducted by the author for more than two years past, certain rather striking "sports" have appeared, which seem to behave as discontinuous hereditary variations. Although sufficient time has not elapsed since their appearance to reveal the exact mode of transmission of these aberrant characters, a brief account of them seems justifiable at present.

PARTIAL ALBINISM

About December 29, 1915, a litter of five young were born, whose parents were brother and sister, both being F_1 hybrids between the subspecies *P. maniculatus sonoriensis* and *P. m. rubidus*. These two subspecies differ conspicuously in color as well as in some other characters, the former race being of a much lighter shade than the latter. Hybrids of the F_1 generation are on the whole intermediate in this respect. Of the five young F_2 mice above referred to, three developed a normal amount of pigment in the skin and eyes, while the other two remained extremely pale. At first glance, this might have been interpreted as a case of simple Mendelian splitting, resulting in the appearance of the grandparental color types. But a close inspection of the pale individuals, as late as the eighth or ninth day after birth, showed that they were nearly or quite pigmentless. Moreover, further breeding of hybrids between these two races has proved that no such simple segregation phenomena occur in the F_2 generation.

Unfortunately, all of the foregoing brood died in very early life, none reaching the age of two weeks. On January 8, 1916, a sister of the above-mentioned mother gave birth to a brood of two, the father being the same as in the preceding case. Both of these F_2 offspring, which are still living, are normally pigmented. But on October 5, 1916, a second litter was born of these same parents. This litter, when first examined, comprized two pale individuals, one of each sex. The skins

of these young mice failed to darken, as happens in normal animals, preceding the outgrowth of the hair, and the pigment of the eyes, which is usually conspicuous at this age, was not in evidence. The hair, at the time of its emergence, appeared nearly white.

Six weeks after birth, these mice, which were still in juvenal pelage, were covered, on the dorsal and lateral surfaces, with hair of a very pale gray shade, very near the "drab gray" of RIDGWAY'S "*Color Standards*," though perhaps a trifle paler. (Two normal F_2 hybrids of the same age varied in shade between RIDGWAY'S "neutral gray" and "dark neutral gray," perhaps averaging the "deep neutral gray".) Viewed from a distance, in the subdued light of the murarium, the "albinos" did not differ widely in appearance from ordinary white mice, but the deeper shade was evident when one contrasted the faintly pigmented lateral region of the body with the truly white hair characteristic of the ventral surface of this species. Other peculiarities of these partial albinos are the complete absence of the black dorsal tail-stripe, the nearly white condition of the ears and the reddish color of the eyes. The latter are far from being of the pink hue found in domesticated white mice and rats, but they nevertheless contrast clearly with the jet black eyes of normal *Peromyscus*. Moreover, they differ notably in size, being smaller, or at least failing to protrude from the head as in the normal animals. Thus the mutation here considered involves several distinct characters, which may, of course, be physiologically related.

At the age of six weeks, a change of pelage was found to be in progress in both of these young mice, though the new hair had not appeared at the surface except in the male. In the latter, the customary replacement of gray by colored hair was evident on the antero-lateral surfaces of the body, but the color in this case was an extremely pale yellow.

Upon the completion of the post-juvenal pelage, some ten weeks after birth, these mice were of a very pale gray shade, suffused with a yellow, which is probably not far from RIDGWAY'S "ochraceous buff" or "cinnamon buff." It would be impossible, however, to express their appearance in terms of any homogeneous shade or tint, covering a continuous plane surface. This second pelage is somewhat darker than the first one, as well as of a different color. In these aberrant mice, as in normal ones, the proximal zone of the hair differs in color from the distal, being of a somewhat "sooty" or "slaty" hue, contrasting with the colored tips. This underlying dusky zone is very much paler, however, in these "mutants" than in the more deeply pigmented animals.

CASTLE (1912) has discussed the finding of a "pure white albino" of

Peromyscus leucopus noveboracensis and the subsequent rearing of several specimens in the laboratory. CASTLE'S mice evidently differed considerably from my own, which are far from being *pure white*. MORGAN (1911, p. 106) describes some nearly white specimens of *P. leucopus ammodytes*, which appeared among his laboratory stock. These animals were apparently black-eyed, however, and retained part of their dark pelage. MORGAN ascribes these changes to some unknown factor in their unnatural environment, acting during the lifetime of the individuals. Whether or not these "mutants" of mine be regarded as albinos or as "red-eyed yellows" is a matter of slight importance for present purposes. Their peculiarities of color obviously depend upon a loss of most of their normal pigment, and this loss affects all of the colored parts of the body. The condition is one which might reasonably be expected to be hereditary, since it has appeared in only two broods, derived from consanguineous matings, the father being the same in the two cases, and the mothers being full sisters. In ten F_2 broods of hybrids between these subspecies, but of other parentage,¹ as well as in three F_3 broods and a number of back-crosses with pure races, no single instance has been observed. The most plausible guess, at present, is that we have to do with a simple recessive character. Fortunately, the two "albinic" mice are of opposite sex, so it is not unlikely that a test of this point will be practicable.

Since the weaning of these two "albinic" young, their mother, mated to the same father, gave birth to two more offspring, both pigmented. Thus, of the six derivatives of this pair of animals, two were albinic, and four normal. Or, counting the brood of five, borne by the other sister, we have four albinos in a total of eleven young. This excess over the expected ratio for a recessive character has, of course, little significance where the numbers are so small.

I am aware of no case in which complete or partial albinism has appeared as a result of the crossing of two strains which were not known to carry this defect, and it is quite possible that in the present instance the association of this phenomenon with subspecific hybridization is purely accidental. On the other hand, hybridization may, as has been contended, tend to call forth germinal disturbances, independently of ordinary Mendelian segregation.

As stated above, no evidences of simple monohybrid segregation have

¹ That is, other parentage on *both* sides. The father was used with various females but no albinos appeared except among the offspring of the two mothers here considered.

appeared among the normal F_2 hybrids between these two races of *Peromyscus*, though I am not yet prepared to report on this phase of the subject.

A YELLOW RACE OF *P. M. GAMBELI*

In September, 1914, a young female of *Peromyscus maniculatus gambeli* was trapped by me on the grounds of the SCRIPPS INSTITUTION, the appearance of which was so exceptional that the skin was saved. The pelage was still juvenal, but instead of having the usual dark gray tone, characteristic of this race in early life, it was relatively very pale. It is hardly possible that the strain described below is descended from the foregoing individual, though both may have had common ancestors within a very few generations.

In the spring of 1916, three peculiarly colored mice were found among the La Jolla *gambeli* stock of the second cage-born generation (" C_2 ," in my notation). They are of a peculiar yellow-brown hue, probably lying between the "cinnamon buff" and the "clay color" of RIDGWAY, and not unlike the most highly colored parts of the hair in *P. m. sonoriensis*. They differ from the latter race, however, in that this richer color covers the entire dorsal and lateral surfaces, instead of being confined to certain areas.² Proximally, the hairs are all of the normal slaty hue. Although no considerable attention was devoted to the first three of these "mutants" until the assumption of the colored pelage, it was noted in at least one case that the latter was preceded by an exceptionally pale juvenal coat.

These "yellow" *gambeli* contrast strongly with the brownish gray characteristic of the normal adults of this subspecies. Indeed, as already said, they diverge more widely from the typical condition of their own subspecies than do mice of a quite distinct subspecies. Thus far very few mice have been observed which show anything approaching an intermediate coat color. The existence of a few animals of somewhat intermediate appearance must be admitted, however, as well as the fact that the "yellows" themselves are far from being absolutely identical in color. The failure to report such departures from the "expected" condition of rigid distinctness is doubtless partly responsible for certain extravagances of neo-Mendelian speculation.

Upon looking over the pedigree of these first three "yellows," it was found that they were the offspring of three different mothers ($C_1 \text{♀} 6$, $C_1 \text{♀} 7$ and $C_1 \text{♀} 77$), and of two different fathers ($C_1 \text{♂} 7$ and $C_1 \text{♂} 49$),

² The color is purest, it is true, on the head and lateral surfaces, the dorsal region being finely streaked with black.

none of which exhibited the peculiarity. It is noteworthy that these three females and two males were all the offspring of a single pair of grandparents (♀46 and ♂16). Besides these five, there were no other offspring of this pair (see figure 1).

Of the two grandparents, one was trapped in the immediate vicinity of the SCRIPPS INSTITUTION, another at a point about a half mile distant. These mice were themselves killed for measurement before the peculiar condition of their descendants was realized. It may be safely assumed, however, that any such condition in the wild progenitors would have been noticed. All of the C_1 and C_2 representatives of this strain have been kept for further breeding purposes, and some other "yellows" have resulted.

At the time of writing, the total number of broods born of the five C_1 mice listed above, is eight. The number of individuals surviving to an age at which the detection of this color peculiarity was possible was eighteen. Of these, twelve were of the normal color and six of the aberrant.³ Thus far, only four of the latter have matured sufficiently to show the definite yellow color of the adults, but this "mutation" appears to be nearly as recognizable in the juvenal as in the post-juvenal condition. In the former state the shade is much paler than the "deep neutral gray," which is characteristic of perhaps the majority of normal young *gambeli*, the difference between the two being most pronounced on the head. In these respects the young "yellows" reared in the laboratory agree closely with the young wild female mentioned at the opening of this section.

In contrast to the proportion of "yellows" appearing in this particular descent line, it must be mentioned that not a single other case has come to light among the four hundred or more cage-born *gambeli* which have been reared to maturity at La Jolla, since the commencement of the experiment. Moreover, with the single exception referred to at the beginning of this section, and a very few which are of somewhat intermediate appearance, no mouse resembling the yellow strain has been noted among the hundreds of these mice which have been trapped locally by my assistants and myself during the past two years.

Only two matings have been consummated in the case of the "yellows" themselves. The seven resulting offspring, while in the juvenal pelage, have agreed in being decidedly paler than the average young *gambeli* of this stage, the body shade being near the "light grayish olive" of

³ The birth of another brood (C_1 ♀6 × ♂49) on March 2, 1917, raises these figures to 14 normal and 7 yellow.

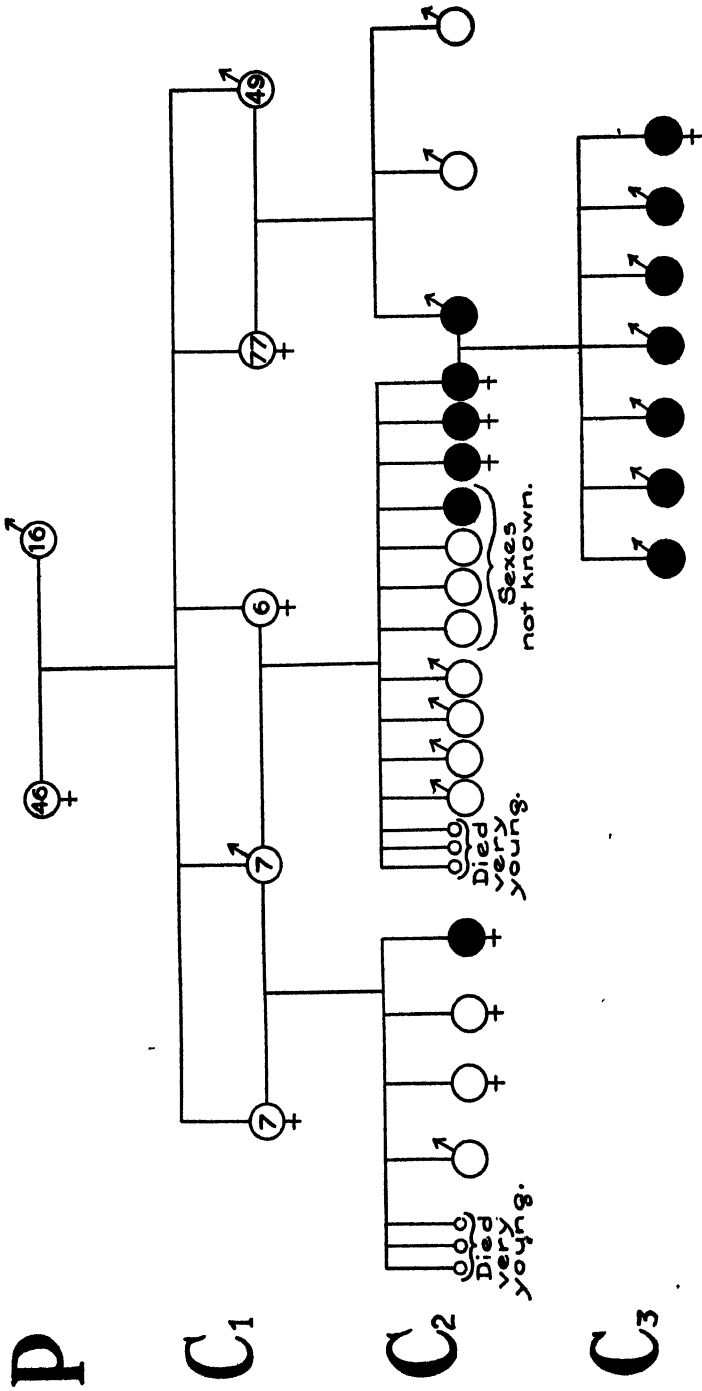


FIGURE 1.—Chart showing pedigree of the "yellow" race of *Peromyscus maniculatus gambeli* now being reared by the writer at the SCRIPPS INSTITUTION. P denotes the original wild parents. C₁, C₂ and C₃ denote the first, second and third cage-born generations. Yellow individuals are designated by circles of solid black, normal ones by open circles. The small circles denote mice whose nature was not determinable, owing to early death.

RIDGWAY, instead of the "deep neutral gray," and that of the head still lighter. On the other hand, they have certainly been darker than were some of the young "yellows" of the preceding generation, and have not been much paler than some exceptional individuals of the normal strain.

At the date of writing, the first-born of the two foregoing (C_3) broods is about four months old, and the three young mice are in the completed post-juvenal pelage. In this second pelage, they are nearly or quite as pale as the yellows of the " C_2 " generation, and differ rather widely from most *gambeli* of their age. On the other hand, they lack, to a large degree, the richer color of the parents, having, in comparison with the latter, a decidedly "washed out" appearance. The divergence from the normal condition is thus less marked in the younger generation than in the older, and this difference between the two is probably not a matter of age.⁴

If we may disregard these possibly significant differences between the C_3 young and their more brightly colored parents, the facts suggest that this aberrant color is a recessive character, dependent on a single factor (or lack of one). Unless I have been a witness to the origin of a *bona fide* mutation, rather than a simple case of gametic segregation, we must suppose that one or both of the grandparents were heterozygous for this character. The five C_1 individuals must all have chanced to be heterozygous, a coincidence, to be sure, for which the chances would have been only one in thirty-two. The ratio 12:6, in the C_2 generation, does not, of course, depart significantly from the "expected" 12:4. In view of the small numbers, the difference may well be accidental.

The question of a possible relation between this "mutation" and the one first discussed is a matter of some interest. To consider only the conditions of pelage color, it might be supposed that the difference was merely one of degree. In the mature state, the one stock is a dark yellow, the other a very pale yellow, in the early life, one is medium gray, the other very pale gray. Some might perhaps suspect that the difference could be accounted for in terms of "intensity factors" or the like. But there would still remain differences between the two strains which could hardly be thus explained, viz., the presence and the absence of the tail-stripe, and the difference in the color and size of the eyes, the latter being quite normal in the "yellows." Without further data, any attempt at a factorial interpretation would of course be premature.

The fact that one of the "mutants" was trapped in nature is of some

⁴The second brood from the same parents approaches the yellow color more nearly. [Note added April 17, 1917.]

interest, since it shows that in this case at least, we are not dealing with a product of artificial conditions. CASTLE (1916, p. 124) states that "yellow sports" have been found among wild meadow-mice (*Microtus*) by COLE, BARROWS, F. SMITH and others. Apparently these have never been reared.

SPECIAL MARKINGS

Various peculiarities in the distribution of pigment in the skin or hair have been observed in individuals of all of my subspecies. Thus the white "star" on the top of the head has been noted in both *gambeli* and *sonoriensis*, some other tufts of white hair on the head of *sonoriensis*, a white terminal segment in the normally black caudal stripe of *rubidus*, as well as peculiarities in the skin pigmentation of the tail and snout of the last-named subspecies and of the feet in all three. Judging from what we know of various other animals, we might confidently predict that some or all of these aberrations would be "genetic."⁵ Indeed, the mode of inheritance of these various peculiarities might prove as worthy of investigation as most of the other subject matter of recent Mendelian investigation.

Since the present studies are only incidentally concerned with the search for "mutations," or an inquiry into their mode of transmission, I can say little as yet regarding the inheritance of these special color markings in *Peromyscus*. In at least two cases, however, there are good reasons for believing that the markings in question are hereditary.

Before discussing the first of these cases, it must be stated that all of the subspecies of *Peromyscus maniculatus* have what is called a "bi-colored" tail, i.e., one in which the hairs of the dorsal surface are dark, while those of the ventral surface are white. Thus there is normally a sharply defined dorsal tail-stripe, varying in width according to the race and the individual.

Now a very few cases have been noted in *P.m. rubidus* in which this stripe terminated in advance of the distal end of the tail, i.e., the terminal portion was white dorsally as well as ventrally. One instance was that of a female of the wild stock trapped near Eureka, California, in which about 2 cm of the dark stripe was lacking. Of the five offspring of this mouse by a normal male, one (a male) showed this character quite clearly, the dorsal tail-stripe terminating about 5 mm in advance of the end (excluding the "pencil").

⁵ CASTLE (1916, p. 125) states that "the production of white-spotted races from small beginnings . . . has been accomplished in the laboratory by CASTLE and PHILLIPS in the case of *Peromyscus*. . . ."

Besides this female, no other wild mouse showing this character has been found among about 250 *rubidus* which I have trapped. But among the first cage-born generation, three others appeared in addition to the male referred to in the preceding paragraph. These last, it is worth noting, were all offspring of a single pair ($\text{♀ } 40 \times \text{♂ } 15$). A fourth mouse of the same parentage was indeterminate in respect to this character, owing to the loss of the tip of the tail early in life. Neither of the parents was recorded as showing this peculiarity, and it is quite unlikely that it would have been overlooked, unless present to a very inconspicuous extent.

If this character is determined by a single "factor," the latter seemingly cannot be a dominant one. If recessive, we must suppose that the mate of the P_1 generation female first mentioned chanced to be heterozygous for this character; also that both parents of the second brood mentioned were heterozygous.⁶ In the latter case, the number of recessive offspring ($\frac{1}{4}$ and possibly $\frac{1}{2}$) is much greater than the expectation, though it is needless to say that such small numbers prove nothing whatever. Indeed, it would be premature to assume a conformity with Mendelian ratios of any sort.

In relation to this aberrant tail character, it is of interest to note that LLOYD (1912, especially pp. 47, 112-116) records the occurrence of a similar condition in the house rat in India, and that he gives evidence for the existence of much restricted local strains in which this character has arisen more than once through independent mutations.

One further peculiarity of an apparently hereditary nature was found in ten or twelve specimens of the first cage-born generation of the subspecies *rubidus*. This was a white tip at the end of the snout, due to the absence of skin pigment as well as to the presence of white hairs. This character, with two doubtful exceptions, was found only among the progeny of two females ($P \text{♀ } 40$ and 41), by a single male ($P \text{♂ } 15$). It is noteworthy that $\text{♀ } 40$ and $\text{♂ } 15$ were the parents of three of the mice with white-tipped tails, and that these three all displayed the snout peculiarity as well as that of the tail. On the other hand, the fourth C_1 mouse having a white-tipped tail had a normally pigmented snout, showing that the two pigment defects are not inseparable.

Unfortunately none of the four C_1 *rubidus* with white-tipped tails has left descendants,⁷ so that the further study of this peculiarity is, for the time being, prevented.

⁶ Unless, indeed, we have to do with the *de novo* appearance of a real mutation.

⁷ Save one in which the tail condition is indeterminate.

About ten cases of white-tipped snouts have appeared in the C_2 generation, and the relationships of these animals implies that this character depends primarily upon genetic conditions. But whether the character is dominant or recessive, or whether it depends upon one or more factors cannot be settled without giving more attention to the matter than at present seems warranted.

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CROSSING OVER WITHOUT CHIASMATYPE?¹

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In a recent number of this journal Professor RICHARD GOLDSCHMIDT has a paper (1917), "*Crossing over ohne Chiasmotypie?*", in which he develops a hypothesis to account for crossing over without recourse to the chiasmatype theory of JANSSENS (which, according to GOLDSCHMIDT, "ziemlich in der Luft schwebt"), or to any similar process.

The argument is based on the "von jedermann anerkannten Voraussetzungen der Chromosomenlehre." Among these Voraussetzungen GOLDSCHMIDT includes the idea that the chromosomes lose their structure during the resting stages, so that it is necessary that the particles be reassembled later to form the chromosomes seen at mitosis. It need hardly be pointed out that this view is not entirely established. Among others, the studies of JÖRGENSEN (1913), BOVERI (1909), BONNEVIE, VEJDOVSKY, and of the students of the "pro-chromosomes," make it at least open to serious doubt. Yet this idea forms the basis of GOLDSCHMIDT's whole argument, for it is assumed that the same mysterious "Kraft" is responsible for the rebuilding of the chromosomes and for crossing over.

However this may be, there are certain points in the further development of GOLDSCHMIDT's hypothesis that seem to me to call for even more critical examination than do his cytological considerations.

On p. 83 he says: "Es ist aber doch klar, dass man jede Proportion geometrisch als Entfernungen auf einer Geraden darstellen kann," and if this representation agrees with the facts, it shows only "dass irgendwelche Kräfte im Spiel sind, deren relativer Effekt als Entfernungen auf einer Geraden dargestellt werden können." Of course any series of proportions can be represented geometrically as sections of a single straight line; but only in certain special cases will such a representation show the relation of the parts to each other. In GOLDSCHMIDT's own imaginary case (pp. 90-91) the relations are not fully represented by placing the

¹ Contribution from the Zoölogical Laboratory of Columbia University and the Carnegie Institution of Washington.

factors in a straight line. The factors *I* and *F*, for example, might be interchanged without appreciably affecting the degree to which the ratios fit. It may perhaps be surmised that the same sort of juggling can be done just as easily with the actual data on which the chiasmatype hypothesis of crossing over is based. This is not the case. In the first place, GOLDSCHMIDT has used for comparison only the data from the first paper developing the linear arrangement idea in detail (STURTEVANT 1913), although these data were at the time stated to be inadequate for certain loci, and have been supplemented by two more recent and extensive tabulations (STURTEVANT 1915, MORGAN and BRIDGES 1916).² Many of the inconsistencies pointed out by GOLDSCHMIDT and by the writer (STURTEVANT 1913), disappear when these later figures are used.

In the second place, the evidence which really puts the linear arrangement and chiasmatype theories on a sound basis is that obtained from experiments involving three or more loci at the same time. This phase of the matter is dismissed by GOLDSCHMIDT with two short paragraphs and a passing reference to the important work of MULLER (1916). These two paragraphs contain calculations for an imaginary experiment involving three loci, *B*, *D*, and *C*. The table on p. 91 gives the observed single crossover values for these three loci as follows:

$$BD = 22.9 \quad DC = 13.0 \quad BC = 25.5$$

GOLDSCHMIDT states, without giving the derivation of the result, that if the three loci are followed in one experiment the result will be:

Non-crossovers	67%
<i>BD</i> singles	20%
<i>DC</i> singles	10%
<i>BDC</i> doubles	3%

If we ignore for the moment the information gained by including *D* in the experiment, the observed crossovers between *B* and *C* will be $20 + 10 = 30$. But *BC* has just been stated to give 25.5. If it is intended to imply that heterozygosis for *D* affects the result, the only comment necessary is that the facts show no such relation to exist. As a matter of fact the values for the *BDC* experiment should read:

(I) Non-crossovers	69.3%
(II) <i>BD</i> singles	17.7%
(III) <i>DC</i> singles	7.8%
(IV) <i>BDC</i> doubles	5.2%

² One of these appeared over a year before GOLDSCHMIDT's manuscript was received, the other a few months before.

These figures and only these, will satisfy the conditions that

- (a) $I + II + III + IV = 100.0$
- (b) $II + IV = 22.9$ (*BD* crossovers)
- (c) $III + IV = 13.0$ (*DC* crossovers)
- (d) $II + III = 25.5$ (*BC* crossovers)

GOLDSCHMIDT declines to discuss the double crossover data further "weil wir glauben dass die STURTEVANT'schen Vergleichszahlen auf Grund einer falschen Formel berechnet sind, und sodann weil es . . . gar nicht unsere Absicht ist, das hier benutzte Schema an Stelle des MORGANSchen setzen zu wollen."

I am unable to understand the bearing of the last part of this statement. It hardly seems necessary to point out that there is *a priori* no reason why a chiasmatype hypothesis should be the only possible explanation of the facts; and there would seem to be no point in developing any particular explanation, unless for the purpose of seeing if that explanation fits the known facts. GOLDSCHMIDT develops his speculation in great detail, until he comes to the really crucial evidence in favor of a chiasmatype view, and then the discussion is dropped. The statement that my formula (for expected number of double crossovers) (STURTEVANT 1915, p. 242) is incorrect seems a scarcely sufficient justification for ignoring that evidence, unless we are told how and why the formula is incorrect. The "formula" in question, when put in terms of symbols, states simply that if a crossover in region *AB* occurs in *p* (a fraction) of the cases, and a crossover in region *BC* occurs in *q* of them, then if the two crossovers are independent they will occur simultaneously (double crossover *ABC*) in $p \times q$ of the cases. This seemed to me to be a perfectly obvious application of an elementary principle of probability, and still seems so in spite of GOLDSCHMIDT's statement that he believes it to be incorrect.

By the use of this simple "formula" it has been found that the crossovers are in fact *not* independent, but that one crossover tends to prevent the occurrence of another one near it. By the same method it has been shown (see especially MULLER 1916) that large pieces of the chromosomes stick together, and *larger* pieces than would be expected as mathematical consequences of the single crossover values. These facts have been emphasized as forming perhaps the strongest evidence in favor of a chiasmatype hypothesis; in fact, they have been used to disprove the supposition "that at a resting stage the chromosomes go to pieces, and the fragments come together again before the next division period.

Linkage might then [be supposed to] mean the likelihood of fragments remaining intact, etc." (MORGAN, STURTEVANT, MULLER and BRIDGES 1915, p. 134). GOLDSCHMIDT, in effect, denies these facts *in toto*. Under the circumstances it seems natural to expect some cogent reason to be given for this denial. No explanation of linkage can have any claim to serious consideration unless it accounts for these facts.

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NUMERICAL EFFECTS OF NATURAL SELECTION ACTING UPON MENDELIAN CHARACTERS¹

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The relation of recent work in genetics to the Darwinian theory is still in dispute. The value of the natural selection hypothesis can only be determined by appropriate experimental tests. At present there appears to be no *inherent* incompatibility between DARWIN'S fundamental principles and the newer concepts of pure lines, mutations, and unit characters. To some the action of natural selection seems to furnish an explanation of the actual trend of organic evolution which is lacking in later theories.

The "pure line" concept does not assist materially in explaining the existing diversity of species. If a pure line remain unchanged indefinitely it is difficult to account for the host of pure lines that exist at present. If, on the other hand, a real variation can occur in a pure line now and again, natural selection would help to explain the trend toward *adaptive* characters which these lines exhibit.

The "mutation" concept may represent the actual nature of variation better than the Darwinian notion of small fluctuating changes. Yet this scarcely affects DARWIN'S main contentions. The *magnitude* and *frequency* of the variations are relatively unimportant, since in any case such variations will accumulate in the course of generations. Their *adaptiveness*, however, is highly significant for biology, and the question remains whether adaptive variations can sort themselves out from non-adaptive by the mere working of natural selection, without the action of a vital force or entelechy.

Finally, the Mendelian concept of "unit characters" in no way precludes the action of natural selection. Indeed it would seem to render easier the submission of the natural selection hypothesis to a crucial experimental test.

It should be noted, however, that the method generally employed in genetic work is not "natural" but "artificial" selection. Experimental-

¹ Written in connection with a course delivered in the Department of Psychology at the Johns Hopkins University.

ists have not generally attempted to measure the relative viability of individuals possessing alternative characters, perhaps the most distinctive feature of Darwinism. In order to determine whether (or to what extent) natural selection is an integral factor in evolution it would seem necessary to observe the changes from generation to generation in the relative proportion of the individuals bearing alternative characters, in a representative population living under natural conditions, and compare the outcome with the effects of natural selection as obtained by calculation. The result should determine whether natural selection actually works, or whether it is masked or assisted by other factors.

The writer has calculated the theoretical effects of natural selection, upon pairs of alternative characters for two special cases. It is assumed (1) that one character is the Mendelian dominant, the other the corresponding recessive; (2) that individuals of one type die off more slowly than those of the other, owing to natural selection, but that neither type is wholly eliminated in each generation.² (3) The general formula would have to consider all degrees of fertility and all ratios of comparative viability between the alternative types. The present calculation assumes *one* fixed rate of reproductive increase only, namely a tendency to double the population within each "generation," and *two* special cases of relative viability—one in which the *dominant is twice as viable as the recessive*, and the other in which the *recessive is twice as viable as the dominant*.

By hypothesis, natural selection occurs only when one of the alternative forms is more adapted to the environment than the other. It is assumed in this discussion that greater *adaptiveness* means greater *viability* or fitness to survive, and that therefore a measure of adaptiveness may be obtained by comparing the numerical proportion of each class in successive generations.

(4) So long as the environment can support the growing population the element of competition plays a minor rôle. But as the population approaches the limit of numbers which the environment will support, competition becomes more intense and adaptiveness becomes more and more of a factor in determining survival. It is assumed that the limit of population which the given environment will support is reached at G_0 ; our calculation begins at this point.

² So far as the writer is aware, previous calculations along these lines deal only with cases in which one form is selected and the other wholly eliminated. (See, e.g., JENNINGS, H. S., "Numerical results of diverse systems of breeding," *GENETICS* 1: 65, 1916.)

Case 1. Dominant fitter. In table 1 it is assumed that the limit of population is 2048 individuals, and that when this limit is reached in G_0 the pure dominants (AA) number 512, the mixed dominants (Aa) 1024, and the pure recessives 512. It is assumed further that these forms are all equally reproductive, that the population tends to *double* in each generation, and that the recessives are only *half as viable* (under competitive conditions) as the dominants (whether pure or hybrid).

By pure chance mating, the number of individuals produced in G_1 will be 1024 AA , 2048 Aa , and 1024 aa . But of these half will die before reaching the mating stage, and the loss of aa 's by hypothesis will be twice as great (in proportion to their numbers) as the loss of AA 's or Aa 's; that is, the loss of aa 's will be 819, of Aa 's 819, and of AA 's 410.⁸ This loss is readily calculated by adding together the number of AA 's plus the number of Aa 's plus twice the number of aa 's and dividing the sum into the limit of population; this gives the "factor of loss" for each of the dominant forms; for the recessive this factor is multiplied by 2.

For example:

G_1	G_2
$1024 + 2048 + 2 \times 1024 = 5120$	$1474 + 1966 + 2 \times 656 = 4754$
Factor of loss = $2048 \div 5120 = 0.4$	$2048 \div 4754 = 0.431$
Whence, loss of AA 's = $1024 \times 0.4 = 409.6$	$1474 \times 0.431 = 635.274$
" " Aa 's = $2048 \times 0.4 = 819.2$	$1966 \times 0.431 = 847.346$
" " aa 's = $1024 \times 0.8 = 819.2$	$656 \times 0.862 = 565.472$

Subtracting the loss from the number of individuals produced in each case we find the number of *reproducing* individuals of each sort in G_1 , which are given under G_1' , and so for each generation. For example:

$$\begin{array}{ccc}
 G_1 & & G_1' \\
 AA \ 1024 - 410 & = & 614.
 \end{array}$$

In order to determine the number of individuals produced in any generation we first find the number of A and a gametes in the "surviving" individuals of the preceding generation; thus, the number of A gametes = twice the AA individuals + the Aa individuals; the number of a gametes = twice the aa individuals + the Aa individuals. Now by chance mating the number of AA individuals in the next generation is proportional to the square of the A gametes in the preceding, the number of aa individuals is proportional to the square of the a gametes, and the number of Aa gametes is proportional to twice the product of A and a ,—the simple binomial formula. But by hypothesis the actual number

⁸ The fractions in the tables are given as the nearest unit. It is found that these slight deviations average up, reducing the error to negligible size in the long run.

TABLE I.
Case 1: In which the dominant form is fitter to survive.

	G_0	G_1	Loss	G_1'	G_2	Loss	G_2'	G_3	Loss	G_3'
$\{AA$	$\{512$	$\{1024$	$410=$	614	$\{1474$	$635=$	839	$\{1910$	$868=$	1042
$\{Aa$	$\{1024$	$\{2048$	$819=$	1229	$\{1966$	$847=$	1119	$\{1774$	$806=$	968
aa	512	1024	$819=$	205	656	$566=$	90	412	$374=$	38
Factor of loss:			0.4			$.431$			$.454$	
Gametes:										
A	2048			2457			2797			3052
a	2048			1639			1299			1044
		G_4	Loss	G_4'	G_5	Loss	G_5'	G_6	Loss	G_6'
$\{AA$		$\{2274$	$1068=$	1206	$\{2560$	$1226=$	1334	$\{2780$	$1348=$	1432
$\{Aa$		$\{1556$	$730=$	826	$\{1356$	$650=$	706	$\{1189$	$577=$	612
aa		266	$250=$	16	180	$172=$	8	127	$123=$	4
Factor of loss:			$.4695$			$.479$			$.485$	
Gametes:										
A				3238			3374			3476
a				858			722			620
		G_7	Loss	G_7'	G_8	Loss	G_8'	G_9	Loss	G_9'
$\{AA$		$\{2950$	$1442=$	1508	$\{3084$	$1515=$	1569	$\{3192$	$1574=$	1618
$\{Aa$		$\{1052$	$514=$	538	$\{940$	$462=$	478	$\{848$	$418=$	430
aa		94	$92=$	2	72	$71=$	1	56	$56=$	0
Factor of loss:			$.4888$			$.4913$			$.493$	
Gametes:										
A				3554			3616			3666
a				542			480			430
		G_{10}	Loss	G_{10}'	G_{11}	Loss	G_{11}'			
$\{AA$		$\{3281$	$1623=$	1658	$\{3351$	$1660=$	1691			
$\{Aa$		$\{770$	$381=$	389	$\{708$	$351=$	357			
aa		45	$44=$	1	37	$37=$	0			
Factor of loss:			$.4945$			$.4955$				
Gametes:										
A				3705			3739			
a				391			357			

AA = pure dominant; Aa = hybrid; aa = recessive.

G_1 , etc. = number produced; G_1' , etc. = number which survive and reproduce.

Assumptions: (1) Population tends to double in each generation; (2) Limit of support is reached at 2048; (3) Recessives are half as viable as dominants.

of individuals produced is twice the number of the producers. Hence we divide each result by the factor 4096 (i.e., the total number of producing gametes, since this has been squared.)

For example:

G_1' gametes	G_2 individuals
$A^2 = (2457)^2 = 6036849$	$AA = 6036849 \div 4096 = 1473.84$
$2Aa = 2 \times 2457 \times 1639 = 8054046$	$Aa = 8054046 \div 4096 = 1966.32$
$a^2 = (1639)^2 = 2686321$	$aa = 2686321 \div 4096 = 655.84$

Repeating this calculation for successive generations (table 1) we find that the pure recessives tend to disappear in 8 generations, that is, the number produced is so small that less than $\frac{1}{4096}$ reach the reproduc-

ing age. The number of hybrids also steadily diminishes, and in the 11th generation amounts to only 0.211 of the pure dominants.

Case 2. Recessive fitter. In table 2 the same assumptions are made, excepting that the recessives are assumed to be twice as viable as the dominants. The calculations are the same, except that here the factor of loss is $AA + Aa + \frac{1}{2} aa$, divided into the limit of population.

For example: in G_2 , $753 + 2006 + 668.5 = 3437.5$

Factor of loss $= 2048 \div 3427.5 = 0.598$

TABLE 2

Case 2: In which the recessive form is fitter to survive.

	G_0	G_1	Loss	G'_1	G_2	Loss	G'_2	G_3	Loss	G'_3
$\{AA$	$\{ 512$	$\{ 1024 - 585 = 439$		$\{ 753 - 450 = 303$	$\{ 488 - 311 = 177$					
$\{Aa$	$\{ 1024$	$\{ 2048 - 1170 = 878$		$\{ 2006 - 1199 = 807$	$\{ 1851 - 1178 = 673$					
aa	512	1024 - 293 = 731		1337 - 399 = 938	1757 - 559 = 1198					
Factor of loss:		.5719		.598						
Gametes:										
A	2048			1756			1413			1027
a	2048			2340			2683			3069
		G_1	Loss	G'_1	G_2	Loss	G'_2	G_3	Loss	G'_3
$\{AA$		$\{ 258 - 179 = 79$		$\{ 96 - 75 = 21$	$\{ 19 - 17 = 2$					
$\{Aa$		$\{ 1539 - 1070 = 469$		$\{ 1062 - 828 = 234$	$\{ 514 - 455 = 59$					
aa		2299 - 799 = 1500		2938 - 1145 = 1793	3563 - 1576 = 1987					
Factor of loss:		.695		.7796			.8848			
Gametes:										
A				627			276			63
a				3469			3820			4033
		G_2	Loss	G'_2	G_3	Loss	G'_3			
$\{AA$		$\{ 1 - 1 = 0$		$\{ 0 - 0 = 0$						
$\{Aa$		$\{ 124 - 120 = 4$		$\{ 8 - 8 = 0$						
aa		3971 - 1927 = 2044		4088 - 2040 = 2048						
Factor of loss:		.97		.998						
Gametes:										
A				4			0			
a				4092			4096			

AA = pure dominant; Aa = hybrid; aa = recessive.

G_0 , etc. = number produced; G'_0 , etc. = number which survive and reproduce.

Assumptions: (1) Population tends to double in each generation; (2) Limit of support is reached at 2048; (3) Recessives are twice as viable as dominants.

$$\begin{aligned}\text{Whence, loss of } AA's &= 753 \times 0.598 = 450.294 \\ Aa's &= 2006 \times 0.598 = 1199.588 \\ aa's &= 1337 \times 0.299 = 399.163\end{aligned}$$

The reproducing population of each sort (AA , Aa , aa), and the numbers of each sort produced in the next generation, are obtained precisely as in case 1.

It is found that the elimination proceeds much more rapidly in case 2, the pure dominants being practically wiped out in the 7th generation and the dominant gametes disappearing entirely in the 8th, so that the selection is then complete.

It is obvious that if the rate of reproduction is greater than the rate assumed here (i.e., doubling between successive generations), the progress of elimination will be more rapid, and conversely if the rate of reproduction is less. Also, if there is a greater difference in viability of dominants and recessives than the ratio here assumed (2:1), the elimination will proceed more rapidly, and conversely. Professor H. S. JENNINGS has indicated to the writer a method of extending the calculation to cover *all* cases by means of a general formula.⁴

Assume:

- (1) That the population at the beginning has reached the limit of numbers that can survive; and call this survival number n .
- (2) The population increases in a constant ratio, such that at each change of generations it becomes l times as great as before.
- (3) The viability of the dominants is to that of the recessives as m to 1. That is, the dominant survives m times as readily as the recessives. (m may be greater or less than unity.)
- (4) Let the population at the beginning consist of $r AA + s Aa + t aa$.

Now, after one reproduction the population will be ln . Since it must be reduced again to n , there must be lost $(l - 1)n$ individuals.

These are to be divided between r , s , and t in the proportions $r:s:mt$ (since t dies m times as readily as the others).

Then the total number of r that die (out of the entire $(l - 1)n$ deaths) will be:

$$\frac{r}{r + s + mt} \times (l - 1)n = \frac{rn(l - 1)}{r + s + mt}$$

Similarly the number of s that die will be:

$$\frac{sn(l - 1)}{r + s + mt}$$

⁴ Professor JENNINGS is responsible for the following discussion (as far as the summary). The writer gratefully acknowledges his kindness in permitting its inclusion here.

The number of t that will die:

$$\frac{mtn(l-1)}{r+s+mt}$$

These values may then be subtracted from r , s , and t respectively to give r' , s' , and t' , the numbers perishing after the selection has occurred.

Then the proportions for r , s , and t in the next generation may be obtained from the following formula:⁵

$$AA = (s + 2r)^2$$

$$aa = (s + 2t)^2$$

$$Aa = 2(s + 2r)(s + 2t)$$

Example.—Case 1: Dominant fitter to survive; generation, G_1 .

Here $n = 2048$

$$l = 2$$

$$m = 2$$

$$r = 1024$$

$$s = 2048$$

$$t = 1024$$

And $l - 1 = 1$

$$r + s + mt = 5120 (= 5 \times 1024)$$

Then:

$$r' = 1024 - \frac{1024 \times 2048}{5 \times 1024} = 1024 - 409.6 = 614.4$$

$$s' = 2048 - \frac{2048 \times 2048}{5 \times 1024} = 2048 - 819.2 = 1228.8$$

$$t' = 1024 - \frac{2 \times 1024 \times 2048}{5 \times 1024} = 1024 - 819.2 = 204.8$$

Case 2 is identical, save that $m = 1/2$ instead of 2; so that $r + s + mt = 3584$ (or 7×512).

SUMMARY

It is found that, assuming a greater adaptation of one Mendelian alternate, either the dominant or the recessive, the more adaptive form tends gradually to "drive out" the less adaptive. The rate of elimination depends on the relative viability of the two forms, as well as on the rate of reproduction of the species. But *the elimination is more rapid when the recessive form is the more viable.*

Adaptiveness may be explained *without the assumption of any in-*

⁵ JENNINGS, H. S., 1916, Numerical results of diverse systems of breeding. GENETICS 1: See p. 65.

herent orthogenetic tendency, if adaptive variations occur as well as non-adaptive. Assuming that by some means real heritable (i.e., mutational) variations *do* occur, whether they be large or inappreciably small, the result in the long run is to select those which fit the species to cope with its environment and to eliminate those which place their possessors at a disadvantage.

It remains to test experimentally whether and to what extent such variations actually occur, and whether the working of natural selection (as above assumed) is masked or reinforced by other more potent factors.

INHERITANCE OF STATURE

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INTRODUCTION

This paper, which it has taken the best part of two years to prepare, has perhaps cost more than the results gained would seem to warrant. Yet so long as the classic topic of heredity of human stature remained insufficiently analyzed, it stood as a constant challenge to the analyst of heredity. If the work has done nothing more than to prove, what might have been anticipated, that the apparent blending inheritance of stature is due merely to the presence of multiple factors it may be justified.

The data upon which this paper is based have been gathered by many hands; but those upon which chief reliance is placed were secured, as stated below, by personal studies made on families, with the assistance of ELIZABETH B. MUNCEY, M.D., Miss MARY T. SCUDDER, of Huntington, N. Y., Rev. W. E. DAVENPORT of Brooklyn, N. Y., Prof. W. S. ANDERSON of Lexington, Ky., the Misses VIRGINIA ANDERSON and LUCILE CRUICKSHANK of Lexington, and Dr. J. D. CROOM of Maxton, N. C. To the host of those who have coöperated in our work, admitting me and my assistants into their homes in Huntington, Patchogue and Brooklyn, L. I., Stamford, Conn., Lexington, Ky., Laurinburg and Maxton, N. C., I would express my thanks for their friendliness. To my assistant, Miss SCUDDER, is chiefly due the reduction of the vast amount of statistical data accumulated. Finally this study could hardly have been possible without the organization of the EUGENICS RECORD OFFICE for the foundation and maintenance of which science is indebted to Mrs. E. H. HARRIMAN.

A. STATEMENT OF THE PROBLEM

I. HISTORICAL

That persons differ in height is one of the most obvious of facts. A moment's consideration suffices to ascribe some of these differences to age (the young are shorter than the mature), others to sex (males are taller than females), and others still to race (the Polish Jews are shorter than the Scotch). There is a wide-spread belief, also, that, within limits, growth in stature may be controlled by conditions of life.

That there are hereditary factors involved in the differences in height of adults follows from the recognition of racial differences, for true racial characters are hereditary. Moreover, this hereditary nature has been popularly long recognized. Thus we are not surprised to find King FRIEDRICH WILHELM I of Prussia, who had an obsession over tall soldiers, planning even to breed them.¹ In the same way CATHERINE DE MEDICI is said to have "caused marriages to be celebrated between male and female dwarfs with the object of producing a dwarf race. Such marriages were; however, uniformly barren" (RISCHBETH and BARRINGTON 1912, p. 358). CHARLES LYELL (1881, I p. 196) writing from France in 1828 says the French troops are

"... a stunted race. By accurate calculation of the height of men of the levy since the peace, it is found that the mean height of Frenchmen has been diminished several inches by the Revolution and NAPOLEON'S wars. These

¹ Details concerning the Prussian Grenadiers are given in the regimental histories. Thus J. BECKER (1885, p. 114) says of the regiment in FRIEDRICH WILHELM'S time: "Die Rekrutierung erfolgte nur durch Werbungen in In- und Auslande. Aber die strenge Zucht und die Vorliebe des Königs für 'lange Kerls' veranlasste die Werbe-Offiziere nicht selten zu harten und unerlaubten Mitteln zu greifen.

"Infolgedessen suchte sich ein nicht geringer Teil der heranwachsenden jungen Männer der gewaltsamen Werbung zu entziehen und ging ausser Landes. Um diesem Uebel abzuhelpen, musste eine Zeit lang in Inlande die Werbung eingeschränkt und fast ausschliesslich auf das Ausland übertragen werden."

Rules as to stature of the men were laid down as follows (BECKER 1885, p. 115): "Ein gute Companie muss also beschaffen seyn: Der Flugel soll von 6 Fuss und über 6 Fuss und der erste Zug von 11½ Zoll auch 11 Zoll und der letzte Mann in ersten Zuge 11 Zoll wenigsten 4 Stiche haben." (The Zoll was about equal to the British inch; 11 Zoll is evidently an abbreviation for: "5 Fuss 11 Zoll").

It is stated that the King contemplated a system of marrying his tall men to tall women but he died before this system was put into effect and his successor FREDERICK THE GREAT was apparently a sexual invert and wished none of his officers married. Thus, according to PRUSS (1832, I, p. 425-6) he was so successful that on the 5th of April, 1778, at Pasewalk in the famous Baireut Dragoon regiment, of all 74 officers, from the Generallieutenant v. BÜLOW down to the youngest Fähnrich not one was married.

are now the sons of those who were not thought by NAPOLEON strong and tall enough to fight and look well."

Such testimony proves that the inheritableness of stature is popularly recognized.

The method of inheritance of stature has long been a matter of scientific interest. In his "*Natural Inheritance*" GALTON (1889, pp. 77, 78, 83, 84) discussed the data on stature that he had obtained from his Records of Family Faculties and from "special observations." A discussion which has led to such momentous consequences as this of GALTON may well be called a "classic." I cannot forbear reproducing here the introductory words of his chapter which treats of stature.

"The first of these inquiries into the laws of human heredity deals with hereditary stature, which is an excellent subject for statistics. Some of its merits are obvious enough, such as the ease and frequency with which it may be measured, its practical constancy during thirty-five or forty years of middle life, its comparatively small dependence upon differences of bringing up, and its inconsiderable influence on the rate of mortality. Other advantages which are not equally obvious are equally great. One of these is due to the fact that human stature is not a simple element, but a sum of the accumulated lengths or thicknesses of more than a hundred bodily parts, each so distinct from the rest as to have earned a name by which it can be specified. The list includes about fifty separate bones situated in the skull, the spine, the pelvis, the two legs, and the two ankles and feet. The bones in both the two lower limbs have to be counted because the stature depends upon their average length."

This quotation well illustrates the complete change of our point of view in studying heredity since GALTON's day. The great multiplicity of elements entering into stature which was for GALTON a "great advantage" for the study of its heredity may well be considered today so great a disadvantage as to render it impracticable to get at the laws of inheritance of stature from available data on stature. Today we recognize the importance of selecting simple clean-cut characters in studying heredity. We recognize that the key to MENDEL'S (1865) success lay in his recognition of this fact. Thus MENDEL says (BATESON 1909, p. 321)

"Some of the characters noted do not permit of a sharp and certain separation, since the difference is of a 'more or less' nature, which is often difficult to define. Such characters could not be utilized for the separate experiments; these could only be applied to characters which stand out clearly and definitely."

However, GALTON exaggerated the number of elements involved in stature, for the length of the vertebræ and intervertebral cartilages depend upon the linear space in the trunk available for their development; they do not determine the length of the trunk.

The method which GALTON used for analyzing the inheritance of this complex character led to important results. It was the thing in GALTON's work that first attracted Professor KARL PEARSON's attention and started him upon the remarkable (even if somewhat misguided) series of papers which rapidly appeared from his pen from 1894 to 1900, and led to the foundation of the "biometric school"—a school whose principles and methods, valuable in certain fields, have shown themselves quite sterile when applied to heredity. GALTON, proceeding by the method of mass statistics, reached the conclusion that children regress from mediocrity about one-third as much as the average of the stature of their two parents does. PEARSON (1896, p. 270) concluded, from a much more elaborate analysis, that the regression of sons on fathers is 44 percent. BROWNLEE (1911) has pointed out that the Galtonian result can be interpreted in modern terms if we assume that stature depends upon several independent factors. In 1911 I pointed out that

"... when the four grandparents are very unlike the adult children will vary greatly in stature, whereas, when the grandparental statures are closely alike, those of the children will be also. When both parents are tall all of the children will tend to be tall; but, on the contrary, if both parents are short some of the children will be short and some tall in ratios varying from 1 : 1 up to 2 : 1" (DAVENPORT 1911).

This conclusion was based on 104 families.

Thus up to the present time no set of original data in stature has been analyzed by modern methods of studying heredity.

II. DEVELOPMENT OF STATURE

The fertilized egg is provided with a mechanism that, in the presence of proper conditions, sets it developing. In the earliest stage—the inhibitory stage—the growth is largely due to a taking in of water. Thus, in the first 14 days of a tadpole's development during which it transforms from a spheroidal egg to an elongated free-swimming tadpole it may gain 22 milligrams of water while it gains only 0.3 milligrams of dry substance; and the proportion of water meantime increases from 56 percent to 96 percent. This is the grand period of growth of the frog (DAVENPORT 1897, p. 75). The grand period of growth in man probably occurs within the first month, perhaps even before the formation of the gill slits. In later growth the additions of water continue to be great but the additions of dry matter are also considerable and increasing so that, in the frog, the proportion of dry matter increases from 4 percent to 6, 8, and up to 20 percent in the adult frog, and 40

percent or more in adult men. This dry substance is largely "formed substance," secreted by active protoplasm. This stage of laying down of dry matter is known as the second or metabolic stage of growth. Anything which advances the metabolic processes, furthers, anything that interferes with them retards, growth and may affect adult size. In the imbibitory stage growth is, within limits, outside the control of the parent. It is the constitution of the egg that controls the rate of its absorption of water.

The metabolic stage of growth in man may be divided into the uterine and the extra-uterine periods. The first period—that of placental attachment—begins at about the time that the gill clefts first show externally. From this time on new building material is brought to the organism from without. During the first 8 weeks of development the embryo increases from 0.0006 grams to 4 grams or 6,000 times. From 8 weeks to 16 weeks it increases from 4 to 120 grams, or 30 times; from 16 to 24 weeks it increases 5 times; from 24 to 32 weeks, 3 times.

Table I (taken from MARTIN 1914, p. 227) gives the successive lengths of embryos and foetuses of 1 to 10 months.

TABLE I
Length of human embryo (vertex to heel) at different ages.

	SCHRÖDER (1893, p. 60)	STRATZ (1907)	MICHAELIS (1906)
End of 1st month of gestation	.7— .8 cm	1 cm	—
" " 2nd " " "	.8—2.5 "	4 "	—
" " 3rd " " "	7— 9 "	9 "	—
" " 4th " " "	10— 17 "	16 "	14.9 cm
" " 5th " " "	18— 27 "	25 "	22.3 "
" " 6th " " "	28— 34 "	35 "	29.5 "
" " 7th " " "	35— 38 "	42 "	33.1 "
" " 8th " " "	42.5 "	45 "	39.7 "
" " 9th " " "	46.7 "	48 "	44.3 "
" " 10th " " "	49— 50 "	50 "	—

Obviously the rate and degree of development of the child during the period of placental attachment must depend to a certain extent upon the quality of the blood of the mother. And, indeed, we find great differences in the weight of the child at term, which are determined both by the length and condition of the body, especially the latter. The weight of living children at birth (in Germany) varies from 2500 grams to 5800 grams; the length at birth from 48 cm to 58 cm (DAFFNER 1902, p. 125). There is, even at birth, a slight sexual difference

(on the average) in the same direction as in the adult. There is also a difference in the average length at birth for different peoples correlated to a certain extent with racial differences in adult size. This is shown in table 2. (Data from MARTIN 1914, p. 228.)

TABLE 2
Length at birth of male and female children of various races.

	♂ cm	♀ cm	Author
Anamites	47.4	46.4	MONDIÈRE
Japanese	49.3	47.8	NAGAHAMA
Russian (from Charkow)	49.5	48.3	ORCHANSKY
English	49.6	49.1	ROBERTS
French (from Paris)	49.9	49.2	MIES
Belgian	50.0	49.4	QUETELET
Great Russian	50.5	49.5	TSCHÉPOURKOWSKY
South Russian Jews	51.2	50.3	DAFFNER

Of 17 infants, who have been born less than a week, measured by me at the JEWISH MATERNITY HOSPITAL, New York City, the total lengths ran (in cm): 54.5, 52, 50.5, 50.5, 50, 50, 50, 49.5, 49, 49, 49, 49, 48, 48, 48, 47.5, 47. Thus the median stature of this series is 49 cm, slightly less than the average found by DAFFNER for South Russian Jews.

With birth begins the second metabolic stage of growth—that of the post-foetal life. The increases in the first few months of post-foetal life are very great and the sexual differences become strongly expressed by the more rapid growth in length of the male. This is shown in table 3, taken from MARTIN (1914, p. 228). For the whole post-foetal period we have a curve of growth such as is given in figure 1.

TABLE 3
Body length of Russian children (from TSCHÉPOURKOWSKY).

	♂ cm	♀ cm
1st week	50.5	49.5
1st month	51.3	50.5
2nd "	53.5	52.8
3rd "	57.0	53.9
4th "	58.7	55.4

This shows that the yearly absolute increments tend in boys to fall off somewhat toward the end of the second year and still more toward the end of the sixth (or seventh) year. Continuing to slow up during

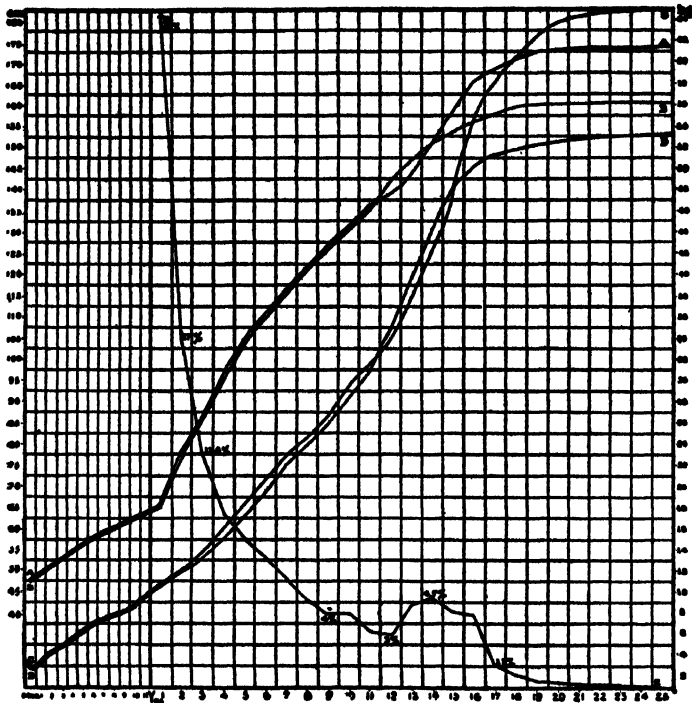


FIGURE 1.—Curves of development, ages being laid off as abscissæ and absolute stature (in centimeters) or weight (in kilograms) being laid off as ordinates. The first 12 months of life are on a different scale ($\times 6$) from subsequent years. Curve AA is that of stature for boys. Curve BB is that of stature for girls. Curve CC is that of weight for boys. Curve DD is that of weight for girls. Curve EE shows for boys the percentage of growth in stature made in the successive years and is especially adapted to showing the periods of retardation and acceleration in growth. From J. W. SEAVER, "*Anthropometry and Physical Examination*."

the ninth year, boys fall in stature behind girls, but at the end of the eleventh or twelfth year the increments increase and continue until the end of the fourteenth year (in the United States until the end of the fifteenth year). This is the period of rapid adolescent growth. The same thing appears in the curve for girls except that there is no slowing up of increments in the ninth year but they go right on holding their own or increasing slightly until the end of the thirteenth year. Consequently they come to exceed the male statures for the ages from 10 (or 11) up to 14 years. After 14, menstruation having begun to set in, the increments of growth fall off markedly, permitting the boys to pass in stature their sisters of the same age.

After the full onset of puberty, which occurs about a year later in boys than in girls, the curve of increments falls rapidly until in girls

at 18 and boys at 20 growth is practically finished. From 20 to 25 years there is, on the average, an increase in stature among males of from 2 to 5 mm, in part depending on race.

The age at which adult stature is achieved varies in individuals. Indeed, as BOAS (1898, p. 1541) has pointed out, variability in stature is exceptionally high between the ages of 13 and 17. DETLEFSEN (1914, p. 120) finds a slight increase in variability of weight of rabbits at 1 year. PEARL and SURFACE (1915) have discovered that the height of the corn plant is more variable at the onset of tasseling. I give an example of such extreme variability in man. Mrs. V., of Huntington, whose stature is 169.5 cm (67.5 inches) stated that she had gained her full height at the age of 13 years. By her husband (165 cm high) she had a daughter whose stature at 17 years was 168 cm, another 163 cm tall at 20 years, and a third whose *stature at 11 years was 160 cm*, or only about 3 to 8 cm short of her probable maximum, though, on the average, an increase of 25 cm to the stature at 11 years is expected.

An examination of the curve of growth brings out this important point that the growth processes which are fairly progressive up to about 14 years, begin to be damped off after that period. Were the average rate of growth of the female between the ages of 8 and 14 maintained up to the age of 25 years, the average woman at that age would be over 210 cm or 82½ inches or nearly 7 feet tall. The reason why we do not reach such a stature is because our growth is damped off; and the principal damping off occurs as the germ glands ripen. Variations in adult stature may conceivably result from an acceleration or retardation in this damping off process.

For, there is a clear correlation, though not perfect, between the average time of onset of puberty and the average age of slowing up of growth and it is probable that the former controls the latter. If one reason why one person is tall and another short is that in the first the onset of puberty is delayed, in the second accelerated, this might come out by asking a number of tall and short correspondents about the age of onset of puberty in their cases, and this I did. But, apparently, data of onset of puberty is a matter of which record is rarely made; so I did not get much satisfaction. In one case, a man of 6 feet 4 inches thought that the onset of puberty was somewhat later than in his brothers. Another, 6 feet tall, thinks that the age of onset of puberty was the same as his shorter brothers, but he has had temporarily a slightly enlarged thyroid. Another (6 ft. 3 in.) says "from childhood

I was always very tall for my age." Equally unsatisfactory are the returns from the under-sized people. One man (J. N. C.) of 5 ft. 7½ in. says he stopped growing when he was about 15 or 16 years of age. Another, much under size, says that having been brought up in the city he had little opportunity for active exercise; but just prior to maturity (at 11 years) he was on his cousin's ranch and grew 7 inches in one year and then he stopped growing almost completely.

There is, on the other hand, abundant evidence that many dwarfs are such because they ceased to grow at an early age and have merely retained their youthful size. In conversation with dwarfs I have secured the following data: The dwarf, JOSEPH ZAINE, was of normal size until 7 years of age when he stopped growing. His stature is now 117 cm which is about that of a boy of 7 years. The dwarf, HELEN L. HASKILL, was of normal weight at birth and developed slowly. At 16 months she weighed about 7.3 kilograms (normal is 8.8 kg). At 12 years she weighed only 10 kg (normal about 30 kg); at 20 she started to grow and at the same time she matured. ANNIE NELSON (Mrs. GEORGE LAIBLE), ateliotic, stopped growing at 7 years and has done little growing since. In addition, many midgets are very small at birth and grow slowly (fig. 19).

III. RACIAL DIFFERENCES IN STATURE

As is well known the average stature attained by men of different races is very varied. It runs from 138 cm (4 ft. 6 in.) in the case of the Negrillo Akkas to 179 cm (5 ft. 10 in.) in the case of the Scots of Galloway. Says DENIKER (1906, p. 30) "the true home of the low stature populations is in Indo-China, Japan and the Malay Archipelago" (under 158 cm or 62 inches). The tall races of the globe are the North-western Europeans, Polynesians, North American Indians and the Negroes of Sudan and adjacent parts of Africa (over 173 cm or 68 inches). The existence of these racial differences of stature is the best evidence that stature depends upon inheritable factors.

IV. SEXUAL DIFFERENCES IN STATURE

In all races of mankind adult men are taller than women and the modal difference is taken as 12 centimeters or 5 inches. This absolute difference between the sexes holds pretty closely for all races, but it is probably still more accurate to state that the male stature is to the female as 100 is to 92, at least for the taller races. This is the difference that GALTON (1889, p. 61) adopts. This difference in the sexes is one that

is characteristic of mammals in general. It is associated with the earlier cessation of growth in the female and with the earlier onset of maturity at which epoch growth is nearly finished.

V. CONTROL OF STATURE BY EXTERNAL AGENTS (NUTRITION)

Variations dependent on this cause are due less to quantity than to quality of ingested food. The studies of OSBORNE and MENDEL (1914) are of great importance here. They find that if rats be fed all they will eat of maize deprived of an amido-acid and tryptophan they will cease to grow and will fall far behind their fellows who have received these materials. It is important to note, however, that if the tryptophan be restored, even after the lapse of months, the little rats start again to grow and eventually catch up with their fellows. That is, the specific growth factor works itself out when it is given a chance despite the prolonged continuation of unfavorable conditions. This is important as indicating the improbability that, in this country at least (and with the class of people with which our statistics have to do) insufficient or improper food counts for much in determining eventual height; temporary starvation has little or no effect on the end result. So, likewise, overfeeding, however much it may affect weight, has probably little effect on adult stature; though it may hasten growth and thus enable a man to reach precociously his predestined stature. The comparative lack of dependence of growth on quantity of food is shown by the fact that a bantam chick which is fed heavily never develops into anything but a bantam fowl.

VI. CONTROL OF GROWTH BY INTERNAL SECRETION

If food conditions have only limited and special relations to growth this is not at all the case with internal conditions. We now know that variation in the amount of the secretions thrown into the body by various ductless glands have important relations to growth. Let us consider some of this knowledge.

Gonads. We have seen how, with the ripening of the germ glands, the rate of growth is temporarily accelerated and then soon brought to a full stop. This intimate correlation between changes in the rate of growth and changes in the functioning of the germ gland suggests that the secretions of the latter influence the former. And it has been suggested that the reason why women are, as a sex, shorter than men, is because maturity (and with it cessation of growth) occurs earlier in women than in men. It is further the result of experience that eunuchs

who are so made before adolescence, tend to grow tall, "leggy" (TANDLER and GROSS 1909), especially in the tibia (PONCET 1903), while at the same time they tend to become obese. Similarly, castrated bulls, or "steers," and cocks, "capons," tend to continue growth beyond ordinary limits. Thus the internal secretions of the gonads play a rôle in limiting growth.

Thyroid. This gland has long been known to exert a control over growth. Insufficient thyroid secretion in children results in undergrowth (cretinism)—a result which may be prevented in some degree if extract of thyroid be given at an early age. I add (table 4) measurements of the stature of a few cretins at Randall's Island, New York City.

TABLE 4
Stature of cretins in comparison with normal of each sex.

Males				
No. and age Stature	(17) 37 yrs 109 cm	(18) 53 yrs 129 cm	Normal ♂ 173 cm	
Females				
No. and age Stature	(8) 21 yrs 134 cm	(7) 23 yrs 125 cm	(3) 27 yrs 133 cm	Normal ♀ 160 cm

The foregoing measurements show a reduction from normal stature in cretins of 37 and 25 percent in the males and of 22, 17, and 16 percent in the females. One may say that cretins fail of realizing about one-fifth of their normal growth.

The *pituitary body* at the base of the brain yields secretions to the blood stream that help control growth and development. When the pituitary body during the growth period secretes in excess, overgrowth occurs "resulting in gigantism when the process antedates ossification of the epiphyses" (CUSHING 1912, p. 25); if it secretes too little (during childhood) there is "skeletal undergrowth, incomplete sexual adolescence and changes in the other ductless glands" (CUSHING 1911, p. 37).

The *pineal body* has a close correlation with growth and the disease of this body in young subjects is associated with increased growth (McCORD 1914; DOCK 1915).

Of the activity of these "ductless glands" there are, of course, all degrees and the suggestion readily occurs that one reason why growth proceeds faster and goes further in one person than another is because

thyroid, pituitary or pineal gland secretes more or during a longer period.

Variations in the secretion of the glands mentioned are very common and, no doubt, hereditary, i. e., racial. The quantity of the secretion varies from time to time with internal conditions and it is affected by severe general diseases such as tuberculosis or syphilis and even scarlet fever, measles, whooping cough and acute articular rheumatism (see DALE 1915). This is the significance of the widespread belief that a given short stature has resulted from a severe infantile disease.

Since growth is so dependent upon secretions that, in turn, are modified by numerous common accidents, one might feel justified in doubting if any inheritance of stature can be traced. On the other hand, it must not be forgotten, first, that the degree to which the functioning of a gland is disturbed by bad conditions is not independent of hereditary factors and also the variations in the ordinary functioning of a gland are determined largely by such factors. Moreover, it appears to be true that the minor disfunctionings of the endocrine glands are unable to prevent the eventual working out of the organism's hereditary growth potentialities. OSBORNE and MENDEL (1914, p. 103) conclude from their experiments that the capacity to grow is not "lost with age, independently of whether it has or has not functioned during the period usually associated with increase in size." Also, the disfunctioning is more apt to exaggerate than to oppose hereditary tendencies. Thus, it is said that "acromegaly affects especially people of large size" (DOCK 1915). In view of all these considerations we have to conclude that the factor of heredity cannot be neglected; it remains to be seen in how far it is determinative.

VII. RELATIVE IMPORTANCE OF CONSTITUTIONAL AND ENVIRONMENTAL FACTORS

There is a strong tendency with certain persons to ascribe idiosyncrasies in stature almost wholly to peculiarities of conditions of development. RIPLEY (1900, p. 85) has fallen into this error in trying to account for the shorter stature of the interior (as contrasted with coastal) cantons of Finisterre on the ground of inferior food supply—forgetting for the moment the difference of blood. Similarly the superior stature of the residents of the state of Kentucky has been ascribed to lime in the soil, and I entertained that hypothesis myself before going to Lexington. The real reason why the people of Lexington, Kentucky, run tall is because they have a large proportion of Scotch

blood, as they readily admit. One can test this conclusion by going to Scotland County, North Carolina. This is on the coastal plain where there is practically no lime. Here, at places like (Mac) Launenburg, (Mac) Queensdale and Maxton (Mac's town) a nearly pure Scotch population is found—descendants of the Cape Fear River immigrants—and they are even taller than the people of Lexington, Kentucky. This experience points strongly to the conclusion that internal constitutional factors are more important than the ordinary environmental differences.

B. INHERITANCE OF TOTAL STATURE

I. STATEMENT OF THE PROBLEM

Although stature is a graduated trait, due to a multiplicity of more or less independently varying elements, yet, owing to the presence of *general developmental factors*, it is possible profitably to consider the relation between the stature of persons in successive generations. Such inquiry will be made both by the mass statistical method of biometry and by the analytical specific-mating method of modern genetics. Our problem is this: By the use of these methods can we detect the presence of specific growth-modifying factors and what is their hereditary behavior?

II. MATERIAL AND METHODS

The material for this study has been drawn in large part from the statements of volunteers made on the "Record of Family Traits" schedules of the EUGENICS RECORD OFFICE and others. Especially must be mentioned a selected list of names and addresses of very tall and very short persons kindly sent us by Mr. ARTHUR HUNTER of New York. To the persons named was sent a special schedule asking for exact height of close relatives, including grandparents, and many data were returned. The quality of these data is doubtless about the same as those of GALTON; the replies on the special schedule are probably more carefully given than on the "Record of Family Traits" schedules. However, these data have their limitations. It is probable that in some cases the height given is merely an estimate; and it is not always clear whether the record is made with the shoes on or off. The presence of special disturbing conditions, such as a slight scoliosis, although sometimes recorded may not always be so. In a word, the material, although valuable because of its extent (it comprises 2354 children of parents whose height is recorded), is not all scientifically precise.

A second lot of data was secured by myself and by my trained assist-

ant, ELIZABETH B. MUNCEY, M.D., using the "Seaver rod," much employed for anthropometric purposes. Further details concerning this material and how it was secured are given below (page 349) where we deal with analytical studies on inheritance of stature.

In studying this mass of data it has been found convenient first to substitute for the actual measurements deviations from the mean of the sex. This mean is taken once for all throughout this paper as: *68 inches (173 cm) for the male; 63 inches (160 cm) for the female.* All statures in this chapter are expressed (to the nearest inch) in terms of deviations from these averages. By this method the sexual differences, which are so important in absolute measurements, may be disregarded.

Also, it is convenient to group the parents into fairly large classes so as to get a significantly great number of offspring to a class. The following classes were adopted:

Very tall, +5 inches and taller	Very short, —5 inches and shorter
Tall, +4, +3, +2 inches	Short, —4, —3, —2 inches
Medium, +1, 0, —1 inches	

All statures are placed in one of these 5 categories: and the terms as used always have the definitions given above. Statures are always assigned to the nearest whole inch. The English system of long measure was adopted because it is in common use in this country and because most of the original data were recorded in this system. However, the measurements made by my assistant and myself were in centimeters and fractions and had to be transmuted for the purpose of this chapter into their English equivalents.

III. MASS STUDIES ON INHERITANCE OF STATURE

I. *Statement of the problem*

Recognizing that there are "growth-as-a-whole" factors, we have to inquire into their nature. It is expected that a comparison of the stature (especially the variability of stature) of the offspring of parents of different statures will throw some light on this subject. For the more variable the progeny of a given class of matings the more numerous the hidden recessive (hypostatic) factors in the germ cells of the parents; the less variable the progeny the fewer the hidden recessive factors. The stature of the parents that have the least variable progeny is probably determined by the presence and activity of the greatest number of *recessive* (or negative) factors, or the absence of the greatest number of positive factors.

2. Results

In our mass studies we have, in the usual biometric fashion, grouped all parental combinations into the same class (without considering the gametic constitution of the parents) and then compared the arrays of children from such phenotypically classified parents. The results are given in table 5. They are not without interest in that they show the distribution of filial statures derived from various matings.

Table 5 shows clearly that the distributions of filial statures differ greatly in the different classes of matings and the averages of the children differ in the same sense as the parents. This is the usual result in graduated characters. Thus when both parents are *very tall* all the children are above the average in stature.² When both parents are *very short* all children, except 1 medium, are short or very short. If both parents are of medium stature the modal stature of the children is the average stature of the population. Of the mating *very short* by *very tall* all offspring (6) are within an inch and a half of the average for the population.

The distribution of the offspring of *tall* (or *very tall*) mated to *tall* (or *very tall*) is characterized by relatively low variability (index of variability, $\sigma = 2.26 \pm .05$). The matings *very short* \times *short* and *short* \times *very short* give a somewhat more variable offspring (index, $\sigma = 2.56 \pm .11$); but the matings *very tall* \times *short* (index, $\sigma = 2.74 \pm .17$) and *very short* \times *tall* (index, $\sigma = 3.22 \pm .22$) and their reciprocals give the highest variability of all.³

The foregoing results are shown graphically in the frequency polygons of figure 2. The fact that the offspring of matings of short persons are more variable than the offspring of tall persons suggests that there are one or more general growth-shortening factors that are dominant over their absence.

3. Selective mating of stature

As table 5, second column, giving the number of each class of matings, shows, the different classes are not equally common. No matings of very tall men and very short women and only 1 case of the reciprocal were found in our records of 879 matings. On the other hand, there

² There is 1 exception in 106 children—the case of a man who is 5 feet 6 inches, or 2 inches below the average. His sister writes: "My brother had a very severe illness when about a year old; we think that is the reason he did not grow as tall as the rest of us." This case is omitted in calculating the filial variability.

³ There are not enough offspring of the mating *very short* \times *very tall* to calculate a significant variability.

TABLE 5

Distribution of filial statures from the given matings, in departures, in inches, from the mean.

Parental mating	Number of matings	F		M		+													Total	Average	σ													
		Average deviation of stature from mean		Average deviation of stature from mean		12	11	10	9	8	7	6	5	4	3	2	1	0				1	2	3	4	5	6	7	8	9	10	11	12	
1. Very tall \times very tall	23	5.782	5.826	1	1	2	10	11	26	12	16	12	8	5	1	[1]													105	6.076	2.380 \pm .11			
2. Very tall \times tall	5	5.848	3.333	1	11	19	21	18	22	17	9	9	2	2	1	2														134	4.403	2.999 \pm .10		
3. Tall \times very tall	71	3.181	5.746	1	1	0	8	21	30	40	45	47	31	27	6	6														263	4.863	2.372 \pm .07		
4. Tall \times tall	91	2.955	2.012	2	11	27	31	53	62	90	53	35	19	8	0	1														392	3.556	2.106 \pm .05		
5. Very tall \times medium	21	5.537	.3809	1	3	4	13	7	14	17	10	8	9														86	3.593	2.201 \pm .11					
6. Medium \times very tall	34	.176	5.764	3	5	5	6	13	22	22	24	21	10	13	3	1	0	2	1	2	0	1							154	3.905	3.149 \pm .12			
7. Tall \times medium	86	2.872	.18604	4	9	16	21	44	48	59	44	34	23	11	6	9	1	0	2	2	0	1						339	2.049	2.541 \pm .07				
8. Medium \times tall	81	.123	2.851	1	3	6	14	13	37	45	38	34	30	20	7	6	2	1	0	2	2	0	1						262	1.954	2.866 \pm .08			
9. Medium \times medium	96	— .0625	.125	1	3	1	26	26	42	53	73	41	31	21	8	4	3														338	0.349	2.247 \pm .06	
10. Very tall \times short	5	5.6	—2.6	1	1	0	1	7	2	7	1	2	1	1	0	1														25	1.486	2.558 \pm .24		
11. Short \times very tall	8	—2.5	5.75	2	1	3	2	2	5	4	5	4	3	0	2														33	1.364	2.889 \pm .24			
12. Tall \times short	33	2.848	—2.656	1	1	3	7	13	12	15	31	19	10	13	10	4	1	0	0	2							142	0.803	2.759 \pm .11					
13. Short \times tall	55	—2.709	2.691	2	1	8	10	17	16	18	27	27	15	15	4	1	2											163	0.495	2.999 \pm .10				
14. Medium \times short	45	—2.045	—2.711	2	3	3	6	12	22	22	27	24	16	4	4	0	2	1											148	—0.527	2.166 \pm .10			
15. Short \times medium	86	—2.709	—1.8604	5	7	23	36	30	46	35	40	23	14	9	2	1											271	—0.295	2.235 \pm .06					
16. Short \times short	52	—2.769	—2.737	1	0	1	0	4	8	18	17	34	27	21	7	5	0	1											153	—1.359	2.334 \pm .09			
17. Very tall \times very short	0																													0				
18. Very short \times very tall	1	—6.0	6.0														4	2														6	+0.667	0.472 \pm .09
19. Tall \times very short	3	2.333	—5.0	1	1	0	1	2	2	3	1	0	0	2														12	—0.290	2.919 \pm .40				
20. Very short \times tall	1	—5.656	2.454	1	1	3	2	2	4	3	4	5	3	2	3	1	1											35	—1.609	3.244 \pm .23				
21. Medium \times very short	8	—25	—5.75	1	1	3	1	5	7	4	2	1	4	2											31	—1.387	2.990 \pm .22							
22. Very short \times medium	23	—6.434	—3.652	1	2	5	2	11	10	11	14	7	13	8	2	1											87	—2.471	2.608 \pm .13					
23. Short \times very short	13	—2.438	—4.916	2	2	2	2	3	5	7	12	5	6	2											46	—3.283	2.243 \pm .16							
24. Very short \times short	22	—6.00	—3.095	1	2	4	1	2	4	1	11	16	10	6	2	4	1	0	0	1						65	—2.815	2.754 \pm .16						
25. Very short \times very short	6	—6.833	—6.00														1	0	0	3	3	2	4	2	0	0	1	18	—5.889	2.404 \pm .27				
Total																			3298															

are 96 matings of the class, medium \times medium. A part of this discrepancy is, of course, due to the greater relative frequency of persons of medium than of extreme stature. But an important part is a consequence of selective mating. Very tall men rarely select very short women not merely because very short women are relatively uncommon (table 5 includes 30 very short mothers) but because such women are selected against by very tall men and are chosen by medium to very short men.

The extent of preference or distaste is indicated in table A by the "preference factor" (pref. fact.) which is the factor by which the "standard proportion" must be multiplied to give the actual relative frequency (rel. freq.) of the mating. For example, 8 out of 50 mothers are very tall; if very tall men married at random 8 out of 50 choices should be of very tall women; actually 23 out of 50 are of very tall women. Since $23 = 8 \times 2.875$, 2.9 is the "preference factor."

Conclusion: Very tall men tend to marry a greatly disproportionate number of very tall women (and few or no very short ones); also tall men marry a disproportionate number of very tall women; medium men tend to marry women of the various statures about in their proportion in the whole population. Short men tend to marry short women and few very tall ones. Very short men marry an excess of short and very short women and relatively few very tall and tall ones. In a word, persons of similar stature tend to marry each other; and extremes are more particular in this respect than those of medium stature.

IV. FAMILY STUDIES

1. *Statement of problem*

In most studies on heredity of stature only parents and children are considered. The parents are considered as a mass and the children as a mass, and the relation of the stature of particular fraternities of children to their particular parents is neglected. Modern genetics has demonstrated the inadequacy, for the study of heredity, of any other method than that of the study of individual families and the consideration of at least 3 generations. The last desideratum is, however, rarely attainable. In a rather extensive experience in the measurement of families I have not once been able to measure two or more grown children, both parents and all four grandparents. Moreover, on account of the shrinking of grandparents in stature, even such complete sets of family statures would not be wholly satisfactory. Not until statures are generally accurately made and recorded for different ages will it become possible—a generation later—to make the desired sort of studies. Meanwhile we shall

TABLE A
*Showing the relative frequency and preference factor of each class of statures to which belong the brides (mothers)
 selected by grooms (fathers) of each class of statures.*

Class		Very tall			Tall			Medium			Short			Very short		
Standard proportion		8			14			18			9			2		
Grooms (fathers)																
Class	Stand. prop.	Freq.	Rel. freq.	Pref. fact.	Freq.	Rel. freq.	Pref. fact.	Freq.	Rel. freq.	Pref. fact.	Freq.	Rel. freq.	Pref. fact.	Freq.	Rel. freq.	Pref. fact.
Very tall	3	23	8.4	2.9	5	1.0	0.3	21	3.4	1.1	5	1.6	0.5	0	0	0
Tall	16	71	25.9	1.6	91	18.8	1.2	86	13.8	.9	33	10.5	.7	3	5.0	0.3
Medium	15	34	12.4	.8	81	16.7	1.1	96	15.4	1.0	45	14.3	.9	8	13.3	0.9
Short	12	8	2.9	.2	55	11.3	.9	86	13.8	1.2	52	16.6	1.4	13	21.7	1.8
Very short	4	1	.4	1.0	.11	2.3	.6	23	3.7	0.9	22	7.0	1.8	6	10.0	2.5
Totals	137	137	50.0		243	50.1		312	50.1		157	50.0		30	50.0	

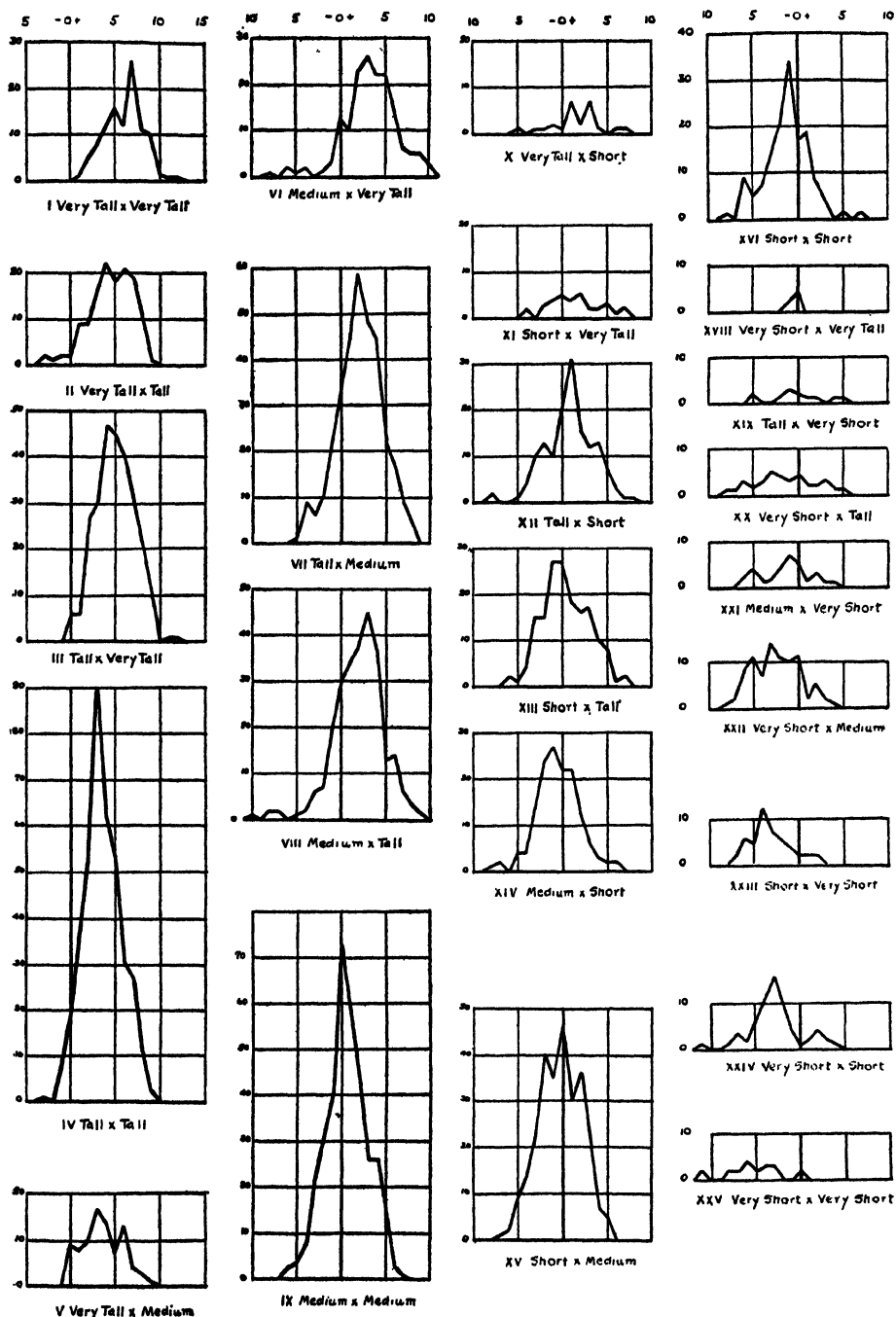


FIGURE 2.—Twenty-four polygons of frequency of the various deviations from the mean stature (for their sex) shown by the progeny of the indicated matings. Abscissae in inches.

have to complete our families by statements of relatives as to their recollection of the stature of the "grandparents."

2. Results

Let us now examine the few matings about which we have full data for 3 generations to learn if possible the nature of the general factors that make for stature. First I give all cases of matings of persons belonging respectively to tall and short strains. By "tall strain" I mean one in which the grandparents, parents and the sibs of the parents are all tall or at least above the average. By a "short strain" I mean one in which the grandparents, parents and sibs of the parents are all short or, at least, below the average. On account of small numbers I have added a few cases that merely closely approximate this ideal. The symbol +, without a figure, indicates "tall"; — indicates "short"; \pm , medium; the number separated from the symbol by a comma gives the frequency.

a. Class I. Both parents tall of tall stock

Mating 1. Both parents are very tall and are at least of tall stock (table 6). This highly selected group of high parental statures (table 6) gives only tall offspring, the average of the children being about the same as the average of the parents. There is here no obvious regression, for the average deviation of the parents is +6 inches (or 5.8 inches) and that of the children is +6.8 inches. Surnames of these four families, so far as known, are: [HAYNES], PATTERSON, HOEING, (Kentucky), HELWIG. Two of these are German names and one is intermarried with a tall Kentucky family in part measured by myself. The other is without significance, as it is a name acquired by marriage. It seems clear that these four families, at least, —all that meet the conditions of "strain"—are without some at least of the shortening factors. All 23 children are at least tall and all but 5 are "very tall."

Mating 2. The fathers are very tall and of at least tall stock; the mothers are tall and of at least tall stock (table 7). The small group in table 7 is less highly selected than the last. It, too, gives almost exclusively at least tall children and shows no regression of deviation of children on parents. Thus the average deviation of the parents is +4.1 and of their children +5.2. The Davis family is from Kentucky and was, in part, measured by myself.

Mating 3. The fathers are "tall" and the mothers "very tall," and the stocks are at least tall (table 8). Table 8 is of special interest in comparison with table 6 for the question of sex-linked factors in statures. But, unfortunately, the numbers are not sufficient to decide the question

TABLE 6
Giving for each family the abmodality of stature (in inches) of father's parents, father, father's sibs, mother's parents, mother, mother's sibs, and the distribution of abmodalities in offspring.

Reference	FF	FM	F	F's sibs	MF	MM	M	M's sibs	+	Offspring	+													
									II	10	9	8	7	6	5	4	3	2	1					
Hay—A	+	+6	+8	$\left\{ \begin{array}{l} \delta: +4, 1; +, 5 \\ \quad: +7, 1 \\ \quad: +6, 2; +2, 3 \\ \quad: +5, 2 \\ \quad: +8, 1; +3, 1 \\ \quad: +9, 1 \\ \quad: +5, 1; +3, 1 \\ \quad: +9, 1; +8, 1 \end{array} \right.$	+4	+3	+5	$\left\{ \begin{array}{l} \delta: +, 2; \pm, 3 \\ \quad: +6, 1; +4, 1; \\ \quad: +2, 1; 0, 1 \\ \quad: +9, 1; +5, 1; \\ \quad: +3, 1 \end{array} \right.$	1	2							1							
Pat—B	+4	+5	+6		+2	+5	+5					5	1		1					1				
Hoeng	+1	+4	+5		x	+13	+7							3	1	1								
Hel—A	+3	+8	+5		+2	+3	+7									1	2	2	1					
Total														1	2	5	1	3	3	3	3	2	3	2

TABLE 8
Giving abmodalities of parental stocks in mating 3, and distribution of abmodalities in the offspring.

Reference	FF	FM	F	F's sibs	MF	MM	M	M's sibs	Offspring										+
									+	9	8	7	6	5	4	3	2	1	
Tow-B	+4	+7	+4	$\left\{ \begin{array}{l} \delta: +1, 1 \\ \varphi: +5, 1 \end{array} \right\}$	+6	+7	+9	$\left\{ \begin{array}{l} \delta: +5, 1; +4, 1 \\ \varphi: +8, 3; +4, 1 \end{array} \right\}$	1	1	1								
Cam-A	+2	+5	+4	$\left\{ \begin{array}{l} \delta: +8, 1, 2 \\ \varphi: +2, 1 \end{array} \right\}$	+4	+4	+5	$\left\{ \begin{array}{l} \delta: +2, 1; \pm 0, 1 \\ \varphi: -5, 1; +4, 1; +3, 1 \end{array} \right\}$	1	1	3	1							
Hil-A	+8	+3	+4	$\left\{ \begin{array}{l} \delta: +2, 1 \\ \varphi: +6, 1 \end{array} \right\}$	+2	+2	+5		1				3	2					
Low-A	+	+3	+4	$\left\{ \begin{array}{l} \delta: +5 \\ \varphi: +1, 4 \end{array} \right\}$	+5	+2	+5	$\left\{ \begin{array}{l} \delta: +4, 1; +2, 2; \\ \varphi: \pm 0, 1; -2, 1 \end{array} \right\}$											
Eld-I	+2	+3	+2		+2	+3	+6						2	2					
Wes-A	+4	+5	+4	$\left\{ \begin{array}{l} \delta: +3 \\ \varphi: +2 \end{array} \right\}$	+2	+3	+5	$\left\{ \begin{array}{l} \delta: +1, 1; \pm, 1 \\ \varphi: \pm, 1 \end{array} \right\}$	1	1	1	1	1	1	1				
Kin-A	+2	+2	+2	$\left\{ \begin{array}{l} \delta: +3, 1; +2, 1; \\ \varphi: +1, 1 \end{array} \right\}$	+8	+5	+5	$\left\{ \begin{array}{l} \delta: +2, 1 \\ \varphi: +4, 2 \end{array} \right\}$					1	1	1	1			
Ben-A	+	+	+4	$\left\{ \begin{array}{l} \delta: +3, 1; +2, 2 \\ \varphi: +1, 1 \end{array} \right\}$	+	+	+5		1				1	3					
Fos-A	+	+	+2	$\left\{ \begin{array}{l} \delta: +1 \\ \varphi: +1 \end{array} \right\}$	+11	+2	+5	$\left\{ \begin{array}{l} \delta: +4, 4 \\ \varphi: +1, 1; +3, 1; \end{array} \right\}$					1		1				
Bea-B	+4	+5	+4	$\left\{ \begin{array}{l} \delta: +4, 1; +2, 1; \\ \varphi: \pm 0, 1; -1, 1 \end{array} \right\}$	+4	+5	+7	$\left\{ \begin{array}{l} \delta: +6, 1; +3, 1; \\ \varphi: +2, 1; +3, 1; \end{array} \right\}$	1				1		1	1	1		
Wil-2	+5	+3	+2	$\left\{ \begin{array}{l} \delta: +7, 1; +6, 1; \\ \varphi: +5, 1 \end{array} \right\}$	+2	+5	+5	$\left\{ \begin{array}{l} \delta: +1, 1 \\ \varphi: +1, 1 \end{array} \right\}$											1
Total										2	5	4	8	to	6	3	3		

the sons is slightly less than the daughters whether father or mother is the shorter.

Again, the average deviation of the offspring shows no regression on that of the parent; for the average deviation of the parents is 4.6 inches and that of the children is 5.4 inches. Here, again, the children of parents who both belong to tall stock are all at least tall.

TABLE 9
Giving abnormalities of parental stocks in mating 4, and distribution of abnormalities in the offspring.

Reference	FF	FM	F	F's sibs	MF	MM	M	M's sibs	+	Offspring	+					
									7	6	5	4	3	2	1	
Mor-A	+4	+6	+4	$\left\{ \begin{array}{l} \delta: +6, 1; +4, 1; \\ \quad +2, 1 \\ \varphi: +7, 2; +6, 2 \end{array} \right.$	+4	+5	+4	$\left\{ \begin{array}{l} \delta: +4, 1; +2, 1 \\ \varphi: +7, 2; +3, 1 \end{array} \right.$	1	2	1	1	1	1	1	
Lak-A	+2	+3	+3	$\left\{ \begin{array}{l} \delta: +2, 1; +1, 4 \\ \varphi: +3, 2; +2, 1 \end{array} \right.$	+2	+3	+4	$\left\{ \begin{array}{l} \delta: +7, 1; +6, 1; \\ \quad +3, 1 \\ \varphi: +4, 1; +3, 2 \end{array} \right.$	1				1	3		
Ric-A	+4	+5	+4	$\left\{ \begin{array}{l} \delta: +6, 1; +2, 1 \\ \varphi: +6, 1 \end{array} \right.$	+4	+3	+3	$\left\{ \begin{array}{l} \delta: +5, 1; +2, 1; \\ \quad +1, 1; -1, 1 \\ \varphi: +5, 1; +4, 1 \end{array} \right.$			1					
Wen-3	+4	+2	+2		+2	+3	+4					1	1	1	1	
Cle-I	+3	+5	+2		+4	+7	+3	$\left\{ \begin{array}{l} \delta: +1, 1 \\ \varphi: +4, 1; +3, 2 \end{array} \right.$				2	4		1	
Get-A	+2	+3	+2	$\left\{ \begin{array}{l} \delta: +2, 5 \\ \varphi: +5, 1; +3, 1; \\ \quad +2, 2 \end{array} \right.$	+6	+4	+2	$\delta: +4, 1$				2	2	2	4	
Wri-I	+5	+7	+3		+2	+3	+2		1						1	
Total										3	3	3	6	8	7	7

Mating 4. Both parents "tall" and of at least tall stocks (table 9). The matings of table 9, though less extremely selected than those of the others, yield only children above the average in stature and practically all tall or very tall. Again, there is no regression; for the average deviation of the parents is +3.0 and that of the offspring is +3.9 inches.

Considering generally the preceding four matings, we see that there

TABLE 10
Giving abmodalities of parental stocks in mating 1 (class II), and distribution of abmodalities in the offspring.

Reference	FF	FM	F	F's sibs	MF	MM	M	M's sibs	— 4	Offspring 5 6 7 8	—
Dav	—	—	8		—	+	7	♂: +, 1	4	2 2	—
Lav	×	×	9		×	×	6		1		1
Lom	×	×	5		×	×	7			1	
Rom	×	×	5		×	×	5		1	1 2 1	1
Total									2 2 2 2 4 2 2		

b. Class II. Both parents short of short stock

Mating 1. Both parents are "very short" and are of short stock (table 10). The data of table 10 are from measurements made by me or my assistant, Dr. ELIZABETH B. MUNCEY, upon certain families of Calabrians. Though the height of the grandparents is not known exactly in any case it is fair to assume that they were much below the average of Anglo-Saxons. The offspring have about the same range of stature as the parents. Their average deviation (—6 inches) is somewhat less than that of their parents (—6.5 inches).

Mating 2. One parent "very short," the other "short." All grandparents below medium. The reciprocals are combined into the one table (table 11). Though table 11 is small it is significant. It seems probable that here again there is a regression toward mediocrity on the part of the children.

Mating 3. Both parents "short" of short stock. This table is, unfortunately, a mere fragment.

Reference	FF	FM	F	F's sibs	MF	MM	M	M's sibs	Offspring		
									1	2	3
Sammelrath	—	—	—3		—	—	—2			1	

c. Class III. One parent of tall stock and the other of short stock

This mating is so important for the theory of inheritance of stature that I have made a special attempt to get examples of it but with slight success. In a few years, when the offspring of the matings of Italian men to Irish women in this country shall have grown up, this study can readily be made. I have only one family, that of LEO MUNAO born in Italy and his wife born in Ireland (of Scotch Irish parentage) and migrated to the United States when a baby, also one son not seen but was

FF	FM	F	F's sibs	MF	MM	M	M's sibs	Offspring		
								0	—1	—2
—1±	+?	—1.3	about ±0	+2?	+3	+5	+4, +1, —3?, +5, +5	1		1?

said by father to be 5 ft. 11 inches (in his shoes?) or +3 inches.

This case turns out not to be very useful; partly because the father's mother was said to be "taller than the father," which would make her 4 inches or more above the average (!) and partly because only one of

the grown children—a girl of 16 years, 160 cm (63 inches)—could be measured.

V. HYPOTHESIS

The tables of offspring of two short parents even of "short stock" show them all to be below average stature but, on the average, less extreme than the parents. This suggests the hypothesis that "*short*" parents may, and frequently do, carry germ cells which lack the shortening factors, while in "*tall*" parents the gametes are more nearly homogeneous and all lack most of the shortening factors.

VI. TEST OF THE HYPOTHESIS

On the hypothesis suggested above there is to be expected a difference in the degree of regression of the children of two tall and of two short parents. To see if there is such a difference we make use of our table 12, comprising all the distributions of children of the various matings. There are 3298 of these children as contrasted with the 928 of GALTON's table 11 in "*Natural Inheritance*," p. 208. The column headed "Regression" is the significant one.

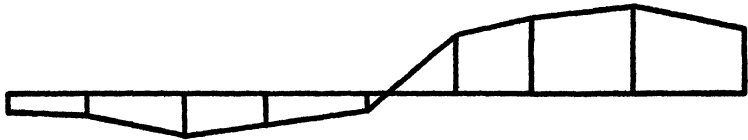
TABLE 12

Matings arranged in order of average departure of parents from medium stature; the average departure of the children of each mating; and the regression of children on parents. + regression means filial regression toward mediocrity; —, filial regression from mediocrity.

Matings	Average departure of parents from mediocrity	Average departure of children	Regression
Very tall × very tall	5.80	6.08	—0.28
Very tall × tall	4.45	4.74	—0.29
Medium × very tall	3.02	3.45	—0.43
Tall × tall	2.93	3.56	—0.63
Very tall × short	1.57	1.41	+0.16
Medium × tall	1.51	2.01	—0.50
Medium × medium	0.03	0.34	—0.31
Short × tall	0.03	0.59	—0.56
Medium × short	—1.45	—0.38	+1.07
Tall × very short	—1.53	—1.28	+0.25
Short × short	—2.75	—1.36	+1.39
Very short × medium	—3.37	—2.19	+1.18
Short × very short	—4.41	—3.01	+1.40
Very short × very short	—6.42	—5.33	+1.09

Table 12 shows clearly that regression of offspring toward mediocrity occurs, as GALTON found, when the parents are much below the average

vt	vt	t	t	m	m	s	s	vs
x	x	x	$x +$	x	x	x	x	x
vt	t	t	m	m	s	s	vs	vs
<i>Par.</i>	5.8	4.4	2.9	1.5	.03	1.4	2.7	4.4



Regr.	.28	.29	.63	.50	.31	1.07	1.3	1.4	1.09
	-				+				

FIGURE 3.—Curve of regression. The ordinates, measured from where the curve cuts the base, give the average parental deviation from mediocrity of each class (Par). The abscissae are proportional to the filial regression (Regr.); real regression is measured up from the base; absence of regression (i.e., *progression*) is measured down from the base line.

in stature. But when the parents are much above the average in stature there is no filial regression; the average of the children is even more extreme than that of the parents (fig. 3). If, now, one looks at GALTON's table, one finds there, too, that regression is most marked in the offspring of short parents; there is little evidence of it in the offspring of the very tallest parents.*

What is the meaning of this difference in regression of the offspring of tall and of short parents? GALTON explained regression as due to "inheritance from the whole population" and not parents merely. To-day we think of regression as due to the presence of recessive genes;

*GALTON's table II gives the following results:

Height of mid-parent in inches	Median value of children's stature	Regression in inches	Height of mid-parent in inches	Median value of children's stature	Regression in inches
Over 72.5	Circa 72.9**	none	68.5	68.2	0.3
72.5	72.2	0.3	67.5	67.6	0.1
71.5	69.9	1.6	66.5	67.2	0.7
70.5	69.5	1.0	65.5	66.7	1.2
69.5	68.9	0.6	64.5	65.8	1.3

**Only 4 entries from which to calculate the average.

genes, that is, which do not influence the phenotype. These recessive factors are commoner in short parents than in tall ones. We may infer that this is because the shorter parents have more dominant factors (and thus conceal more recessive allelomorphs) than taller parents. For taller parents, whose stature is determined largely by recessive factors, carry in their germ plasm less that is not expressed than do shorter parents. Hence resemblance to parents in stature is greater in the progeny of tall parents than in the progeny of short ones.

A second test of the hypothesis is found in the size of the index of variability (i. e., σ , the standard deviation).

TABLE 13

The standard deviations of the stature of offspring from the various matings arranged in order of size.

Mating	σ	$E\sigma$	Mating	σ	$E\sigma$
Tall \times very short	3.22	$\pm .22$	Medium \times short	2.41	$\pm .06$
Very tall \times medium	2.80	$\pm .09$	Very short \times very short	2.40	$\pm .27$
Very tall \times short	2.74	$\pm .17$	Very tall \times very tall	2.38	$\pm .11$
Tall \times short	2.67	$\pm .07$	Short \times short	2.33	$\pm .09$
Tall \times medium	2.66	$\pm .05$	Medium \times medium	2.25	$\pm .06$
Medium \times very short	2.65	$\pm .12$	Very tall \times tall	2.25	$\pm .05$
Short \times very short	2.56	$\pm .12$	Tall \times tall	2.11	$\pm .05$

Table 13 shows that the least variable offspring are those of two tall parents; also that matings of similars give rise to less variable progeny than matings of dissimilars. Thus tall \times tall, medium \times medium, short \times short, very tall \times very tall, very short \times very short, are found in the lower half of the table and tall and very short, very tall and short, tall and short in the upper part of the table.

The meaning of this result is not perfectly clear, but it is about what would follow if parents of all classes are somewhat heterozygous, i. e., carry recessive factors. Then the recessive factors will be expressed phenotypically in a smaller proportion of the offspring when the parents are similar than when they are unlike; in the same way and for the same reason that among the offspring of 2 heterozygous brown-eyed parents only 25 percent have blue eyes, while from a simplex brown-eyed and a blue-eyed parent 50 percent of the progeny have blue eyes. In both cases the unlike matings give rise to the greater variability in the progeny. CASTLE and PHILLIPS (1914, p. 30), MULLER (1914, p. 574) and MACDOWELL (1916, p. 729) show that increased variability in F_1 is evidence of the presence of multiple factors.

From this table we see that the mating *medium* \times *medium* gives rise

to a relatively slightly variable progeny. Now, since medium stature is often the product of *tall* \times *short* it might be expected that the progeny of this mating would be especially variable. That such is not the case is probably due in part to the fact that most "medium" parents are not heterozygous for the extremes of stature. First, there exists, no doubt, a "medium" biotype which is more commonly represented in this country than any other; and, just because of its commonness, is less apt to be heterozygous than the short biotype. Extremes of tall and short offspring do, indeed, sometimes arise from two mediums but the pure mediums are so much more common than the hybrid mediums as to give the high concentration at the mode that is actually found.

Table 13 gives the standard deviation as a measure of absolute variability. But it is clear that, other things being equal, we should expect the individuals of a tall race to show more absolute variability in stature than those of a short race for the same reason that one expects a greater absolute variability in a series of measurements of a kilometer than of a dekameter. A fairer measure of variability would seem to be the coefficient of variability in which variability is expressed in units of the average height. The coefficients of variability are given in table 14, arranged according to size.

TABLE 14

Coefficients of variability of offspring of various classes of matings arranged in a decreasing series of size.

Mating	Coefficient of variability	Mating	Coefficient of variability
Tall \times very short	.0483	Medium \times tall	.0380
Very short \times medium	.0402	Medium \times short	.0357
Short \times very short	.0394	Short \times short	.0350
Very tall \times short	.0394	Medium \times medium	.0329
Medium \times very tall	.0392	Very tall \times very tall	.0321
Short \times tall	.0390	Very tall \times tall	.0310
Very short \times very short	.0384	Tall \times tall	.0294

Table 14, more even than table 13, proves the relatively slight variability of the progeny of tall parents. In the upper part of this table short parents occur twice as often as tall while in the lower half of the table tall parents occur twice as often as short.

VII. SUMMARY AND CONCLUSIONS

Analysis of the data thus shows:

1. That similar matings yield in F_1 a less variable progeny than dis-

similar matings; and this is evidence that both tall and short parents carry a number of unlike factors for stature.

2. Among similar matings, the progeny of two short parents are more variable than the progeny of two tall parents; and this is evidence that short parents carry in the gametes a greater number of unlike factors for stature than do tall parents.

3. Regression of the filial stature toward mediocrity is absent when the parents are selected for great stature, but markedly present when the parents are short. This proves that the gametes of tall parents are less varied (more extreme) than those of short parents.

As we have seen, low variability of progeny indicates that the genotypic factors of the parents are the recessive factors. The limiting case is that of parents of whom both show a monohybrid recessive trait; *all* of the children of such will be alike and show the recessive trait, while, on the other hand, if both parents show the dominant allelomorph and are heterozygous the children will vary greatly. It seems reasonable to conclude, therefore, that tall parents are such in consequence of the absence of certain dominant growth-repressing factors, rather than that short parents are such by an absence of positive, growth-promoting factors. One may conclude that shortness is due to certain positive factors that inhibit growth of the various parts.

C. INHERITANCE OF THE SEGMENTS OF STATURE

I. STATEMENT OF THE PROBLEM

We have, hitherto, in this paper, considered stature as a whole. But, as we have seen, stature has been recognized since GALTON's day as the resultant of numerous more or less independent variables. It is, in any case, a graduated character, is often cited as the most typical case of such, and is probably more often used than any other to illustrate variation in accordance with the binomial curve of frequency of variation.

During the last few years much attention has been paid to the inheritance of graduated or quantitative characters, in the studies of NILSSON-EHLE (1909, 1911), EAST (1910, 1916), LANG (1911, 1911a), EAST and HAYES (1911), EMERSON (1910, 1916), BELLING (1912, 1915), EMERSON and EAST (1913), CASTLE et al (1909), GOODSPEED (1912, 1913, 1915), MACDOWELL (1914), PHILLIPS (1912, 1914), TAMMES (1911), DAVENPORT (1911, 1913) and many others, and the theory that graduated characters result from multiple factors has become more and more firmly established.

I. *Correlation between segments of stature in the adult*

That human stature (or, indeed, the length of any animal) should prove to be a simple trait is hardly to be expected for the reasons already set forth. CASTLE (1914, pp. 51, 52) has, however, developed the idea that

"... to a large extent the factors that determine size are *general* factors affecting all parts of the skeleton simultaneously. . . . Whatever special factors (if any) there are, which are concerned in limiting the size of particular bones, these can play only a subordinate part in determining size. The chief factors are plainly general factors and control the growth of the body as a whole."

The evidences upon which this conclusion is based are, for rabbits, correlations obtained between the length of various bones as follows:

Occipital to maxilla <i>and</i> zygoma posterior.....	0.750
Occipital to maxilla <i>and</i> length of humerus.....	0.743
Occipital to maxilla <i>and</i> length of femur.....	0.760
Occipital to maxilla <i>and</i> length of tibia.....	0.702
Length of zygoma posterior <i>and</i> humerus.....	0.675
Length of zygoma posterior <i>and</i> femur length....	0.674
Length of zygoma posterior <i>and</i> tibia length.....	0.658
Length of humerus <i>and</i> femur length.....	0.857
Length of humerus <i>and</i> tibia length.....	0.791
Length of femur <i>and</i> tibia length.....	0.858

It will be noted that the high correlations are between head length, or head width (zygoma) on the one side and length of a leg bone on the other. Such pairs of dimensions do not enter into human stature. PEARSON and his co-workers calculated various correlations for man, some of which are very high; but these are mostly either between symmetrical organs, like right and left femur, or else between stature and one of its components, like femur length. Between stature and femur the correlation is 0.37; between clavicle and scapula, 0.12 to 0.16. On the other hand, PEARSON does find a high correlation between two independent elements of stature, viz., femur and tibia. This is given as 80 percent in the male and 89 percent in the female. But these determinations were made from a small amount of material (50 individuals of each sex) that was not at all homogeneous in age. I have had access to measurements of about 260 Harvard students taken by Dr. SARGENT and his assistants, made on men who were mostly 18 or 19 years of age. From these measurements the obviously undeveloped individuals

have been excluded. The correlation between "knee height" and "pubic arch" minus "knee height" is only 24 percent, with a probable error of 4 percent. That this correlation is so much less than PEARSON'S (80 as contrasted with 24) is in part due to the fact that the knee height includes height of ankle, which is independently variable.

The correlation of all that stands above the "pubic arch" and all that stands below is also not high in the Harvard measurements, being only about 30 percent. That supra-pubic and sub-pubic portions of stature are to a certain extent dependent is obvious from the fact that "midgets" retain nearly the average proportion of parts. On the other hand, that they are to a certain extent independent is demonstrated in achondroplastic dwarfs in whom the trunk is of nearly normal size but the legs have failed to grow with the rest of the body (fig. 4). Marked differ-



FIGURE 4.—"Cretinous" dwarf, representing the achondroplastic, short-legged type. From MARTIN 1914, p. 211.

ences in relative length of supra-pubic and sub-pubic portions of stature are seen in the anthropological "races." Thus the Australians and some negro groups have a relatively short trunk and long legs (fig. 5) while among Mongoloids, Eskimos, and some Amerindians the trunk is relatively long and the legs short (fig. 6).

The segments of the supra-pubic region—i. e., the supra-sternal and

sub-sternal—are independently variable. I find a correlation between them of only 9 percent, with a probable error of $\pm 4^4$ —a very small correlation.

The segments below the pubic arch, i. e., knee-to-pubic and knee-to-



FIGURE 5

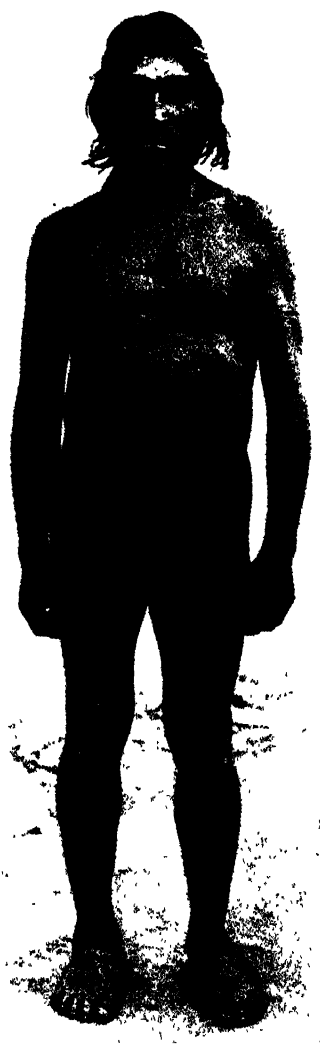


FIGURE 6

FIGURE 5.—Dinka negro. Photo. FRITSCH. From MARTIN 1914, p. 263.

FIGURE 6.—Chiriguan Indian. Photo. LEHMANN-NITSCHKE. From MARTIN 1914, p. 263.

⁴ All the correlations were calculated independently by three persons: J. A. HARRIS, MARY T. SCUDDER and C. B. DAVENPORT.

sole, have, as stated above, a correlation of 24 percent with a probable error of ± 4 . That the correlation of these two segments is not high we might expect, since certain persons have a relatively long thigh and others a relatively short thigh. The relatively long thigh is said to be the European type, here it constitutes about 50 percent of the whole leg length, while the fore leg is 41 percent and the ankle height 9 percent. A relatively short thigh is characteristic of the anthropoid apes. In the Chinese of Setschuan the thigh constitutes 48 percent; the fore leg 43 percent and the foot 9 percent of the leg (MARTIN 1914, pp. 314-15). In relation to total body length, the length of thigh varies in different races from 27 percent in Badeners to 23 percent in Japanese and Bugu of Africa. The lower leg varies from 24 percent among the Sikhs and certain African tribes (the Lobi, 25.7 percent) to 22 among the Badeners and Japanese.

Between standing and sitting height in the Harvard measurements there is a correlation of $0.64 \pm .03$. The proportion that sitting height is of stature varies in racial average. Thus sitting height is 53 percent of stature among Norwegians, 54 to 49 percent among various tribes

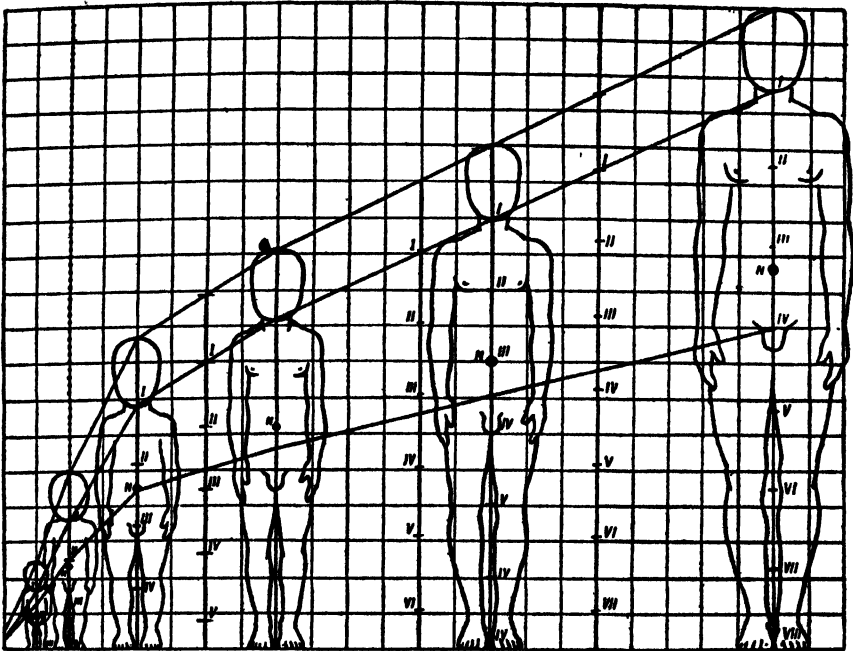


FIGURE 7.—Diagram showing absolute changes in total stature and length of segments of stature before birth, at birth (dotted line), at 2, 7, 12, and 20 years of age. Lines connect the vertices, chins, and middle points of stature of each figure. The principal vertical lines are spaced, using the head (vertex-chin) length as a unit. After STRATZ, from MARTIN 1914, 257.

of Africa and 46.5 among Australians. As HRDLICKA (1909) has shown, the proportional sitting height of adult races tends to decrease as the total stature of the race increases; this is well shown among the San Carlos Apaches (table 15, from MARTIN 1914, p. 260).

TABLE 15

Showing proportion of sitting height to total height in Apaches of both sexes and of various statures.

Total height in cm	Proportion of sitting height to stature		Total height in cm	Proportion of sitting height to stature	
	♂	♀		♂	♀
110 — 119.9	55.1	55.8	140 — 149.9	52.3	53.3
120 — 129.9	54.6	54.2	150 — 159.9	52.1	53.5
130 — 139.9	53.8	53.8	160 — 169.9	52.3	52.4

The conclusion that follows from a consideration of these data is that general factors control growth only to a degree that may be estimated as less than half. On the other hand, special factors are present that control, independently, the growth of the various elements that go to make up stature. And the graduated nature of the variations of stature must be largely due to the number of these independently varying units.

In view of the considerable independence in variability of the segments of stature, we are not surprised at our failure to find any simple "Mendelian" laws of inheritance of stature as a whole. Accordingly, it seemed desirable to study the inheritance of the different segments of stature.

2. *Developmental changes in relative length of segments of stature*

A casual comparison of an infant and a grown person suffices to show that the relative length of the segments of stature changes with age (figs. 7 and 8). Thus at birth, the length of head from vertex to chin is about 25 percent of the whole stature; in the adult it is about 12 percent. Similarly the length of leg is about 35 percent of stature in the infant and nearly 50 percent in the adult. The midpoint of stature is above the navel in the infant and below the "sacral arch" in the adult. Relatively, during development, head-and-neck changes least; the trunk next and the legs most of all.

In consequence of this change in proportions of the segments of stature—a change which does not cease altogether until after puberty—it is as impossible in family studies to make use of the proportions of undeveloped children as it is of their absolute dimensions.

II. MATERIAL AND METHODS

The difficulties in the way of getting precise data on the inheritance of the elements of stature are truly formidable. No collection of such data for *families* is, so far as I know, extant, and they can only be collected by specially trained persons. Also, there are obvious limitations to the detail of measurement that can be secured. To supply the deficiency in some degree the writer personally visited numerous families in the nearby village of Huntington, Long Island, and the city of Lexington, Kentucky, also among Italians in Brooklyn, New York, and secured their coöperation in his investigation. Dr. ELIZABETH B. MUNCEY, M.D., also assisted in measuring Italian families in Brooklyn and some families in Stamford, Conn., and Patchogue, Long Island. Except for a few measurements made by Miss MARY T. SCUDDER of Huntington and Miss VIRGINIA ANDERSON and Miss LUCILE CRUICKSHANK of Lexington, all measurements were made by these two persons. The measurements were made by a "Seaver rod" manufactured by the NARRAGANSETT MACHINE COMPANY of Providence, R. I. Measurements were made mostly without shoes, but in a few cases the height of the heel was obtained separately and subtracted from the total stature.

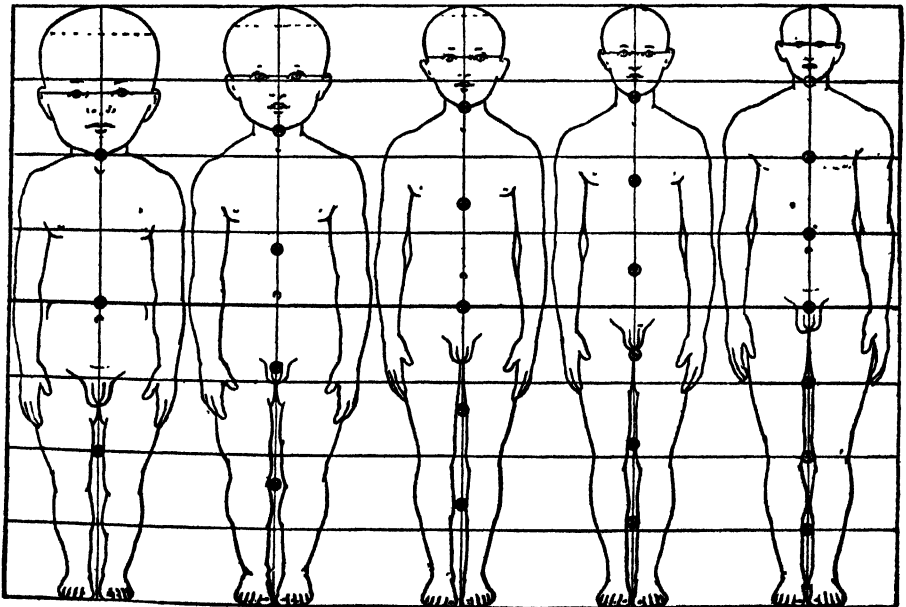


FIGURE 8.—Five outline human figures illustrating the changes in proportions of parts during development, total stature in all cases being taken at 100. The stages are selected such that the stature is respectively $\frac{1}{4}$, $\frac{1}{3}$, $\frac{1}{2}$, $\frac{2}{3}$, and $\frac{3}{4}$ of face length. The proportional rise of the half-stature point from the navel to the pubis is shown by the heavy horizontal line. After STRATZ, from MARTIN 1914, p. 257.

The measurements were as follows:

1. Stature, either in stocking feet or with heel and sole subtracted;
2. Sitting height, from a flat chair seat to vertex;
3. Torso, from a flat chair seat to upper end of sternum (manubrium);
4. Height of fibula head (attachment of external lateral ligament) from floor.

From these measurements head and neck length is got by subtracting 3 from 2; and "femur" by the formula: (No. 1) — (No. 2) — (No. 4).

Since in this section we shall have often to deal with deviations from average or standard lengths of segments and with deviations from standard proportions it is desirable to give a table of such standards as have been adopted in this paper. This is done in table 16.

TABLE 16

Standard (average) length of the different segments of stature, in centimeters, and percentage that each is of the total stature.

Name of measurement	Average length in centimeters		Percentage of stature
	♂	♀	♂ and ♀
Stature	173	160	100
Sitting height	91	85	53
Head and neck	32	29	18
Torso	59	56	35
"Femur"	37	34	21
"Fibula"	45	41	26

All data, with names and addresses, are permanently filed at the EUGENICS RECORD OFFICE.

III. MASS STUDIES ON VARIATION IN PROPORTIONS OF SEGMENTS OF STATURE

Human body stature has two clearly distinct portions—the trunk (including head and neck) and the legs. The proper dividing line between these two portions of stature is the upper edge of the symphysis pubis, because it lies at the same level with the head of the femur, i. e., passes through the center of the acetabulum. While it is quite practicable to determine the height of this line in gymnasia this is not practicable in homes with persons ordinarily dressed. The next best thing is to get *sitting height* which in a person of average stature is close to 10 cm greater than the vertex-symphysis dimension. Conversely the total stature minus sitting height is about 10 cm less than symphysis-sole height, or the total leg length.

The relative symphysis height and trunk + head length are given in table 17 (MARTIN 1914, p. 256) for various races. The figures for the two sexes (which are always closely similar) are here averaged.

TABLE 17
Racial differences in symphysis pubis height and trunk + head.

	Symphysis height	Trunk + head		Symphysis height	Trunk + head
Bushmen	53.0	47.0	Poles (also Belgians)	50.7	49.3
French	52.2	47.8	Whites of United States	50.3	49.7
Menangkabau-Malays	51.9	48.1	Kalmucks	50.1	49.9
Negroes of United States	51.8	48.2	Laplanders	50.0	50.0
M'Baka negroes	51.5	48.5	English	49.9	50.1
Kossacks	51.4	48.6	BaBinga	49.1	50.9
Tartars	50.7	49.3			

The ratio of sitting height to total stature (cural index) is naturally larger than that of trunk + head to stature. Some figures for different races, from MARTIN (1914, p. 260), are given in table 17 A.

TABLE 17 A
Giving for 4 races the ratio of sitting height to total stature.

Sitting height		Sitting height	
BaBinga negroes	53.6	English	52.4
Russian Jews	53.3	Belgian (also Norman-French)	52.3

In our families of English, Italian and German stock the range was from 50.6 to 57.5 percent and the mean about 53.0 for non-Italian and 53.5 for south Italian families.

The length of the trunk is measured by the distance between the symphysis pubis and the upper end of the episternum. This is a dimension that varies relatively as well as absolutely during development. Thus, from MARTIN (1914, p. 261, after SCHWERZ) we have for inhabitants of Schaffhausen the absolute and relative lengths of the trunk in the male sex shown in table 18.

TABLE 18
Trunk length and various ages.

Age-years	In centi- meters absolute	Ratio $\frac{\text{trunk length}}{\text{stature}}$	Age-years	In centi- meters absolute	Ratio $\frac{\text{trunk length}}{\text{stature}}$
6-7	33.8	29.6%	14-15	43.6	28.8
8-9	35.7	29.4	16-17	46.3	29.4
10-11	38.8	29.1	18-19	47.3	28.8
12-13	39.3	28.4	Over 20	49.5	29.3

Thus the trunk is relatively short at the age of 12 to 13 years. This

relative length of the trunk is different in different races. Again, following MARTIN (1914, p. 262) we have as in table 19:

TABLE 19
Ratio of trunk length to stature in various races.

Race	Percent	Race	Percent
Japanese of high rank	34.2	Mawambi—Pigmies of Africa	31.2
Australians	33.4	White Russian Jews	30.5
Chinese	33.1	Men of Baden	30.3
United States		French	29.4
(Amherst students)	31.8	Swiss	29.3

Figure 9 gives the relations between pubic height, trunk, and total stature in a number of young men (students at Harvard College) measured at the gymnasium under the direction of Dr. DUDLEY A. SARGENT. The measurements were made without clothes and are probably highly reliable. The range of pubic height is from 43.6 to 56.5

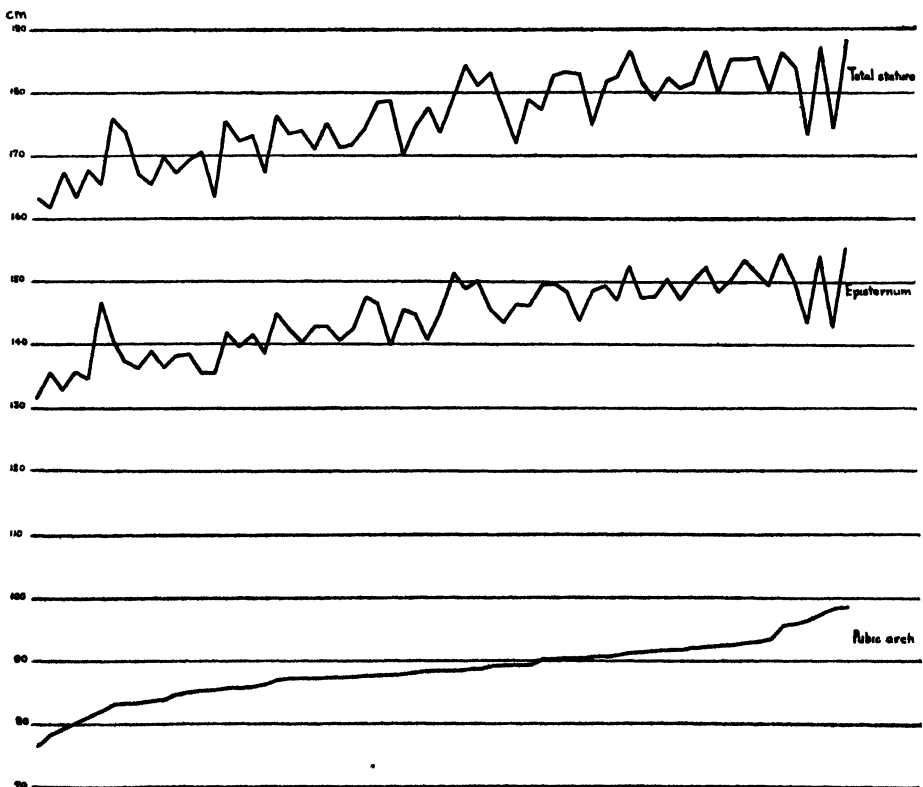


FIGURE 9.—“Ogive” curve of “pubic” heights of Harvard students with correlated height of “episternum” and total stature. The ordinates give lengths in centimeters.

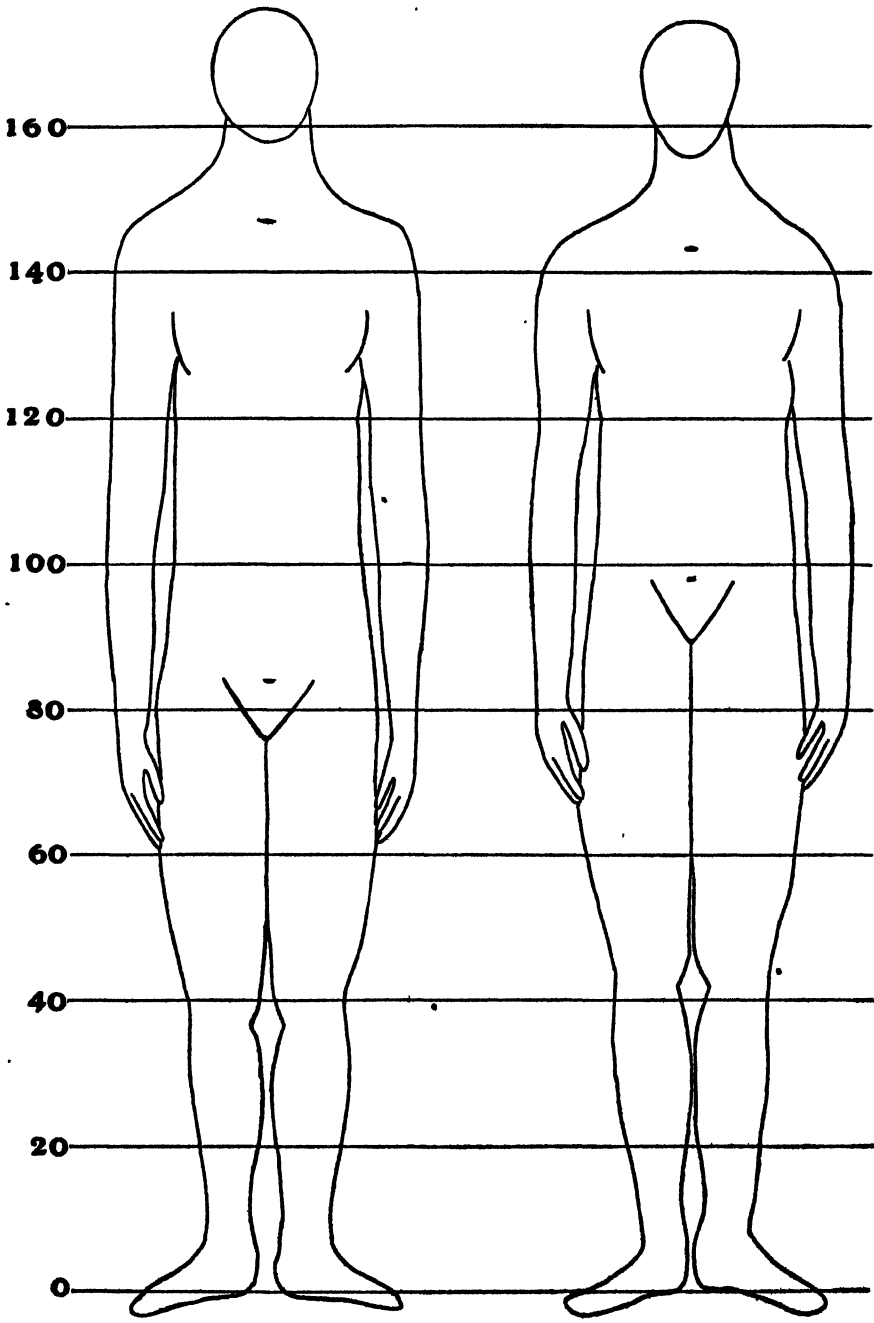


FIGURE 10.—Outlines of two males, aged about 20 years, each about 176 cm tall and selected for extreme unlikeness in torso length.

percent of the stature. The ratio of trunk length (i. e., symphysis pubis to episternum) to stature varies from 35 to 25.5 percent; the remainder of stature, the head and neck, is typically from 18.4 to 16.4 percent of the stature. Outlines of two of the individuals plotted in figure 9 who differ most widely in relation of torso length and height of pubic arch are given in figure 10.

IV. FAMILY STUDIES

The data for the studies in heredity of segments of stature were, as already stated, specially collected. They were originally all expressed in metric units and so this system is used in this section of the paper. As the segments selected were torso, fibula, head and neck, and "femur," our data will be discussed under these heads, except that "femur" being merely a residue, not an actual measurement and not agreeing with the length of the femur or thigh, this segment is not specially analyzed.

We shall first consider the family distribution of the absolute measures (or rather their deviation from mediocrity) of the 3 segments, and then the family distribution of the proportions that each bears to the whole stature.

1. *Inheritance of absolute length of stature segments in terms of deviation from the median*

a. Torso length

Discussion. Table 20 indicates that when *both* parents show long or short or medium torso, their children show the same, on the average. When one parent has long and the other short torso the children have (on the average) a torso that is shorter than the average torso of the whole population; a torso with average length of -1.78 cm from mediocrity. Again, long (or very long) \times medium (thrown together) give children with torso a little (1.56 cm) above the average, but the mating short (or very short) \times medium gives children that deviate strikingly from the mean in the direction of shortness. For, medium \times very short gives a filial average of -3.18 cm and even medium \times short a filial average of -1.56 cm. Short acts as though it is relatively stronger toward medium than is tall toward medium; a result that we should expect if "short" carried dominant factors.

As for the comparison of the filial standard deviation, this is complicated by the fact that (on account of small numbers) it has been necessary to make the parental range greater in some cases than in others.

TABLE 20

The distribution of frequencies of torso lengths in the children when the parents belong to the respective 8 stature groups represented. The filial measures are expressed in centimeters.

Deviation from mean of children, in cm	Eight groups of parental statures							
	1	2	3	4	5	6	7	8
	L × L VL × L L × VL VL × VL	VL × M L × M M × L M × L	VL × S L × S S × L S × VL	S × M M × S	S × S	VS × M M × VS	S × VS VS × S	M × M
+11								1
10				1				
9	1							
8	2	1						
7	1	1						
6	2	1						2
5	1	3	1	1				1
4	2	9		1	1			4
3	2	3		2	2		2	4
2	1	3	1	7	3			6
1	2	6	5	11	9	1	2	10
±0	1	6	2	18	7	1	3	7
-1	1	4	3	9	9	3	1	12
2		2	6	13	8		1	18
3		1	3	12	15		1	9
4		1	2	14	13	2		10
5		1	1	8	16	1	5	5
6		1	1	5	6	1	3	5
7				1	9	2		2
8			1	1	3		1	
9			1					
10								2
<i>n</i>	16	43	27	104	101	11	19	98
<i>Av. Dev.</i>	+4.125	+1.558	-1.778	-1.558	-2.970	-3.182	-2.58	-1.286
<i>σ</i>	2.95	3.08	2.98	2.83	2.81	2.76	3.28	3.38

Thus, in the first column the parents are either very long or long (a group of wide range), but in column 5 both belong to the group of "short" (a group of slight range). Despite this, we can draw certain conclusions. Thus short × very short mating gives nearly the greatest variability of all and there are two offspring with a deviation of +3 cm and about 37 percent show a deviation of 0 or higher. On the other hand, the offspring of the long matings are practically all long (1 case of -1 cm) and only 13 percent have a deviation of 0 or under. The "short" group seems clearly to carry more recessive factors than the "long" group.

It is noteworthy that the progeny of two parents with medium torso should be clearly more variable than progeny of the mating very long

(or long) \times short as 3.38 is to 2.98. This suggests that medium torso is not overwhelmingly commoner than long or short but that, on the contrary, the group of heterozygous mediums constitute an important fraction of the medium group; so that the progeny, through segregation of long and short components, are exceptionally variable.

b. Fibula length

Let us now consider the distribution of fibula length in the progeny of parents of selected fibula length (table 21).

TABLE 21

Distribution of fibula length in the progeny of parents of selected fibula length as indicated at head of each column.

Deviation from mean in cm— children	Ten groups of parental statures									
	1	2	3	4	5	6	7	8	9	10
	L \times L VL \times L L \times VL VL \times VL	VL \times M M \times VL L \times M M \times L	VL \times S S \times VL L \times S S \times L	S \times M M \times S	M \times VS VS \times M	S \times S	S \times VS VS \times S VS \times VS	M \times M	L \times VS VS \times L	VS \times VL
+11	1									
10	1									
9		1								
8	2	1								
7	1									
6	2	3	1	1						
5	2	1						3		
4	8	8	2	1				2		
3	4	13	1	3	1	2		5		
2	3	18	7	10	2	2		9		1
1	2	16	8	10	1	2	1	10	2	
0		16	8	14		3		11	2	1
-1		14	8	27	2	12	1	7	2	1
-2		12	3	15	2	12	4	6		
-3			1	6		9	5	5		
-4		1		4	1	2	5	2		2
-5			2	2		2	2	2		
-6						1	2			
-7						2	1			
-8							3			
-9										
-10										
-11							2			
n	26	104	41	93	9	49	26	62	6	5
Av. Dev.	+4.53	+1.16	+0.34	-0.56	-0.22	-1.82	-4.54	+0.23	0	-1.40
σ	2.58	2.29	2.03	1.95	2.20	2.14	2.97	2.39	0.82	2.33

Discussion. Table 21 shows that when both parents have long fibulas or both short fibulas or both medium fibulas they have progeny which, on the average, are like themselves respectively.

In this table the mating very long \times very short gives chiefly short

progeny and long \times long matings give no short; while short \times short matings give about one-fifth of their progeny of mean or taller stature.

The greatest variability (2.97) is found in the offspring of short (or very short) \times short. Long \times long gives variable offspring but largely due to an extension in the positive end of the series. Short \times medium gives in this case the lowest variability (1.95) but this cannot properly be compared with the very long (or long) \times medium, with its greater parental range.

The variability of the progeny of the mating very long (or long) \times short is in this case rather low (2.03) as compared with the variability of the progeny of two mediocre parents. This is as we found it in table 20.

c. Head and neck length

We have now to consider the distribution of length of head and neck in the progeny of parents of various classes of head and neck length.

Discussion. In table 22 we see that when both parents have a long suprasternal segment few or none of the progeny are medium or below

TABLE 22

Showing distribution of head and neck length in the progeny of parents of the nine classes of head and neck length, indicated in the tops of the columns.

Deviation from mean in cm—in children	Nine groups of parental statures								
	1	2	3	4	5	6	7	8	9
	VL \times L L \times L L \times VL VL \times VL	VL \times M M \times VL L \times M M \times L	VL \times S L \times S S \times VL S \times L	S \times M M \times S	S \times S	VS \times M M \times VS	S \times VS VS \times S	M \times M	VS \times L L \times VS
+10		1							
8								1	
7		2						1	
6	1	3		1				1	
5	3	3	1	3	1			1	
4	2	13	2	2	1			5	
3		4	1	6	5	1		10	
2	2	16	4	16	2		1	11	1
1	1	14	3	23	9	2	4	17	1
± 0		16	1	17	6	2	3	21	
-1	1	8	1	27	9	4	4	14	3
-2		3		20	11	2	7	8	1
-3		2	1	4	2	4	5	3	
-4		1	1	2	3	1	1		
-5		1		2	1	1	1		
-6						1		1	
-7				1					
-8							1		
-10				1					
-15							1		
<i>n</i>	10	87	15	125	50	18	28	93	6
Av. Dev.	+3.30	+1.48	-1.27	-.10	-.34	-1.67	-2.41	+0.69	+0.33
σ	2.10	2.16	2.41	2.29	2.20	2.19	3.56	2.16	1.37

(1 in 10, or 10 percent), but when both parents have a short suprasternal segment many of the children are medium or above (24 in 50, or 48 percent).

The most variable progeny are the offspring of short \times very short parents; the least variable progeny are derived from very short \times long matings. Next in size is from the very long (or long) \times long matings ($\sigma = 2.10$); the medium \times medium matings produce a slightly more variable progeny ($\sigma = 2.16$).

d. Summary

The examination of tables 20-22 shows conclusively first that the length of each segment of stature is more or less dependent on hereditary factors and that parents with short segments carry factors for long segment (or absence of shortness) more often than long segments carry factors for short segment. Thus in table 19 very long (or long) \times long yields 12.5 percent of progeny 0 or shorter while very short (or short) \times short yields 24.2 percent of progeny 0 or longer. In table 21 very long (or long) \times long yields no progeny (in 26) who are 0 or shorter; but very short (or short) \times short yields 10 in 75 (or 13.3 percent) who are 0 or taller. In table 22 very long (or long) \times long yields 1 out of 10 (10 percent) 0 or shorter; while very short (or short) \times short yields 41 percent 0 or longer. Thus in very short (or short) \times short matings a full quarter of the progeny have the medium length of segment or longer. One cannot from these figures, however, reach any conclusion as to the number of factors involved.

The tables show also that, on the whole, the parental short lengths yield a more variable progeny than the parental great lengths; and that matings long \times short have progeny with a relatively low variability. This result (which is not found in stature as a whole) is a familiar one in genetics and indicates that in the segments of stature we are approaching a condition of relatively few factors for the character.

2. *Independence in inheritableness of segments of stature*

a. Strains characterized by idiosyncrasies of particular segments

The observations recorded in the preceding section suggest that the lengths of the different segments of stature are inherited independently as is indicated particularly by the absence of a high correlation in their variability. If this is true we may expect to find strains characterized by idiosyncrasies of particular segments, and this proves, indeed, to be the case. Below, I give some examples from the families which are especially measured for this study.

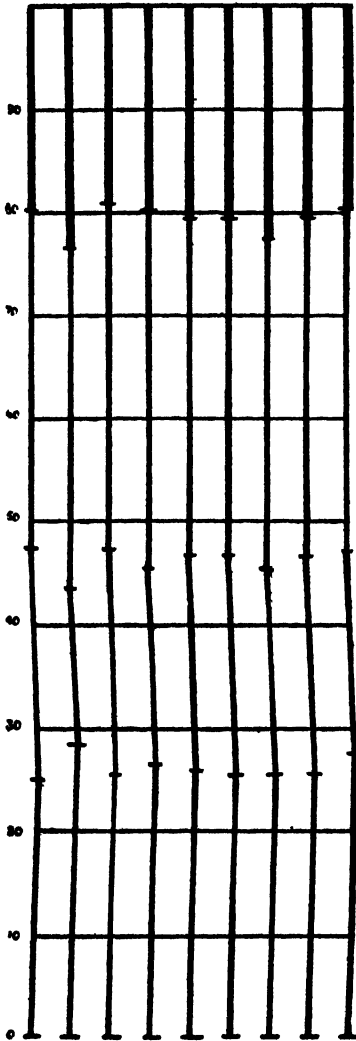


FIGURE 11

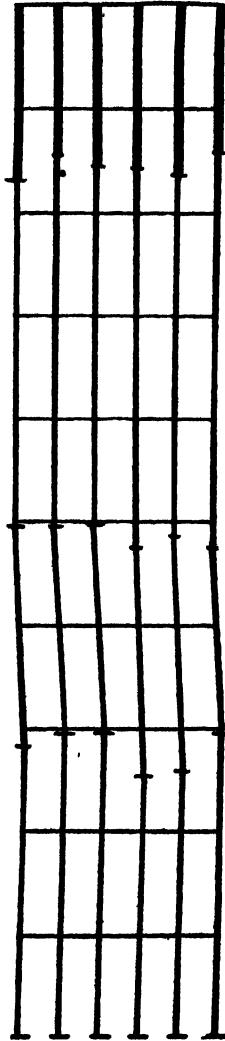


FIGURE 12

FIGURE 11.—Diagrams of proportions of segments of stature in a family characterized by long head and neck. The first diagram on the left is that of the father; the second, that of the mother; the remainder, those of the progeny.

FIGURE 12.—Diagrams as in figure 11, except of a family characterized by short head and neck.

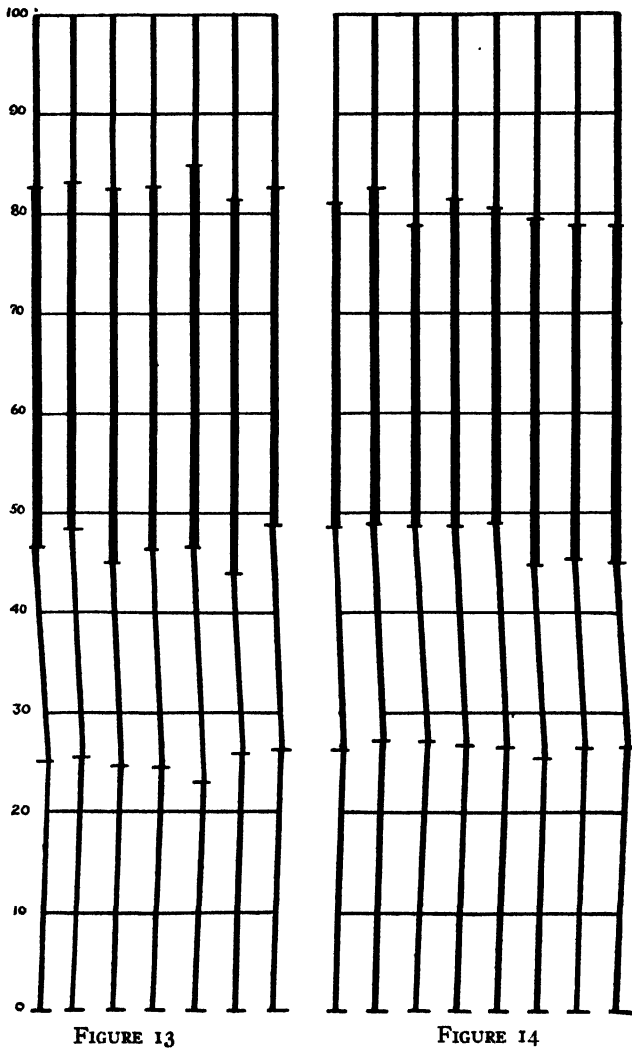


FIGURE 13.—Diagrams as in figure 11, of a family characterized by long torso.
FIGURE 14.—Diagrams as in figure 11, of a family characterized by short torso.

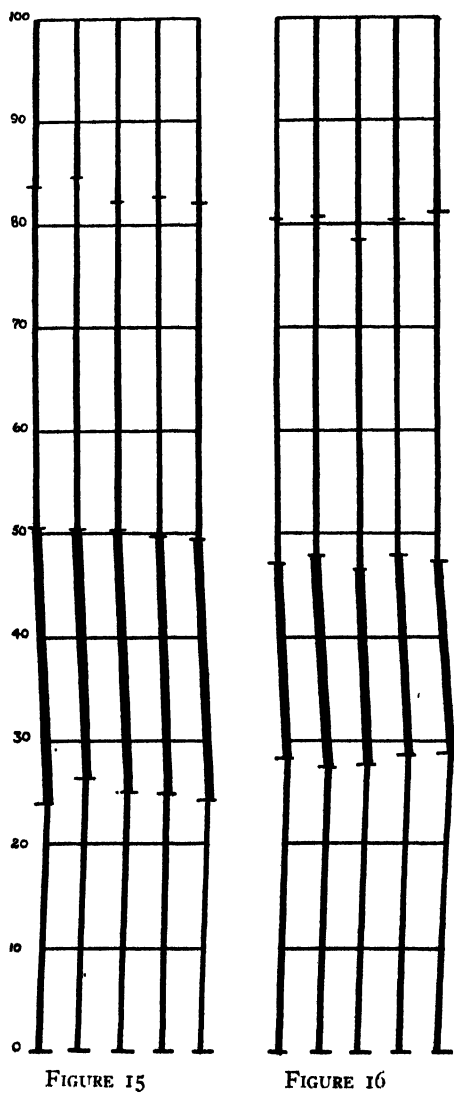


FIGURE 15.—Diagrams as in figure 11, of a family characterized by long thigh.
FIGURE 16.—Diagrams as in figure 11, of a family characterized by short thigh.

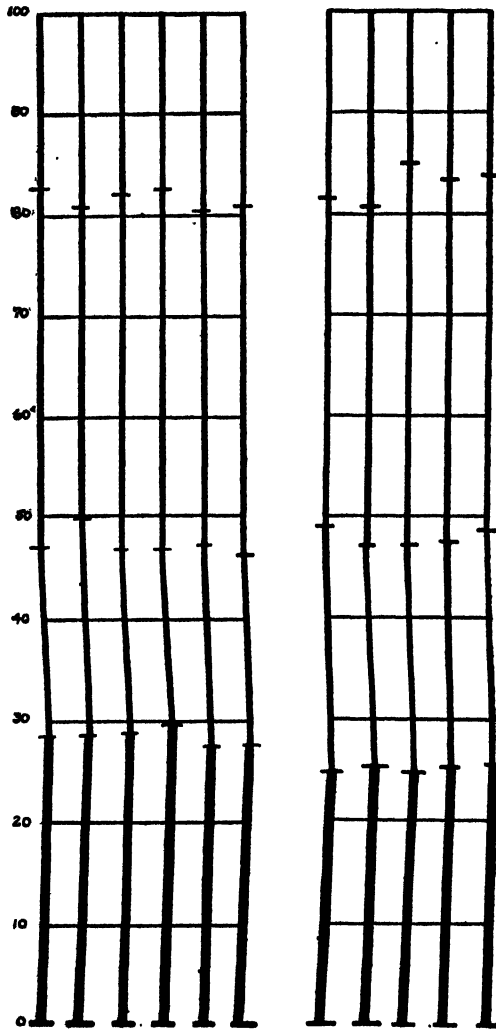


FIGURE 17

FIGURE 18

FIGURE 17.—Diagrams as in figure 11, of a family characterized by long fibula.

FIGURE 18.—Diagrams as in figure 11, of a family characterized by short fibula.

TABLE 23

Strains characterized by idiosyncracies of particular segments.

a. Long "neck + head" (fig. 11).

Cre., W.	F: 32.7 cm (+0.7); M: 30.5 cm (+1.5) dau. 1, 34.5 cm (+5.5); dau. 2, 32.8 cm (+3.8); dau. 3, 32.7 (+3.7)
Hog., E.	F: 34.5 cm (+2.5); M: 34.2 cm (+5.2) dau. 1, 34.6 cm (+5.6); dau. 2, 3.6 cm (+4.6); dau. 3, 30.2 cm (+1.2)
Rob.	F: 33 cm (+1.0); M: 33.2 cm (+4.2) son 1, 34 cm (+2.0); dau. 1, 29.4 cm (+0.4); son 2, 36 cm (+4.0)
Wal., M.	F: 33 cm (+1.0); M: 36.5 (+7.5) son 1, 35.5 cm (+3.5); son 2, 36.2 cm (+4.2); son 3, 39.3 cm (+7.3); son 4, 34.9 cm (+2.9); dau. 1, 31.0 cm (+2.0); dau. 2, 32.7 cm (+3.7); son 5, 30 cm (—2) [at 14 years].

b. Short "neck + head" (fig. 12).

Cal.	F: 29.6 cm (—2.4); M: 28 cm (—1.0) son 1, 25.2 cm (—6.8); dau. 2, 27.0 cm (—2.0)
Lav.	F: 26.0 cm (—6.0); M: 25.5 cm (—3.5) dau. 1, 26 cm (—3); son 1, 30 cm (—2.0)
Rou., A.	F: 31.1 cm (—0.9); M: 26.6 cm (—2.4) son 1, 30.7 cm (—1.3); son 2, 30.3 cm (—1.7); dau. 1, 26.8 cm (—2.2)

c. Long torso (fig. 13).

Gal., F.	F: 63 cm (+4); M: 57.5 cm (+1.5) dau. 1, 63 cm (+7); son 1, 65 cm (+6); son 2, 63.4 cm (+4.4); son 3, 66.5 cm (+7.5)
Hol., J.	F: 61.5 cm (+2.5); M: 57 cm (+1) son 1, 62 cm (+3); son 2, 63 cm (+4)

d. Short torso (fig. 14).

Bay., D.	F: 52 cm (—7); M: 53 cm (—3) dau. 1, 51 cm (—5); dau. 2, 51 cm (—5); son 1, 57 cm (—2)
Bay., J.	F: 58.3 cm (—0.7); M: 51.7 cm (—4.3) dau. 1, 52.3 cm (—3.7); dau. 2, 53.5 cm (—2.5)
Cha., O.	F: 56.4 cm (—2.6); M: 53.4 cm (—2.6) dau. 1, 54.1 cm (—1.9); dau. 2, 49.7 cm (—6.3); dau. 3, 49.9 cm (—6.1)
Con., J.	F: 55 cm (—4); M: 50.5 cm (—5.5) son 1, 52 cm (—7); son 2, 54.2 cm (—4.8); dau. 1, 52.7 cm (—3.3); son 3, 54.4 cm (—4.6); son 4, 55 cm (—4); dau. 2, 49 cm (—7)
Par. (Ital.)	F: 53.5 cm (—5.5); M: 49 cm (—7) son 1, 54.5 cm (—4.5); son 2, 52.0 cm (—7); son 3, 58 cm (—1); dau. 1, 52.5 cm (—3.5)

e. Long "femur" (fig. 15).

Bar., H.	F: 37.7 cm (+0.7); M: 36.2 cm (+2.2) dau. 1, 37.4 cm (+3.4); dau. 2, 35.2 cm (1.2)
Hur., R.	F: 38.5 cm (+1.5); M: 35 cm (+1) dau. 1, 35.7 cm (+1.7); son 1, 46 cm (+9)
Woo., W.	F: 44.4 cm (+7.4); M: 42.2 cm (+8.2) son 1, 46.4 cm (+9.4); son 2, 45.1 cm (+8.1); dau. 1, 43.1 cm (+9.1)

TABLE 23 (continued)
f. Short "femur" (fig. 16).

For., W.	F: 29.5 cm (−7.5); M: 31.5 cm (−2.5) dau. 1, 27.5 cm (−6.5); dau. 2, 25 cm (−9)
Gil., L.	F: 28 cm (−9); M: 32.8 cm (−1.2) dau. 1, 27.5 cm (−6.5); dau. 2, 33.3 cm (−0.7); dau. 3, 30.8 cm (−3.2); dau. 4, 31 cm (−3)
Rom. (Ital.)	F: 35.4 cm (−1.6); M: 28.5 cm (−5.5) son 1, 32.2 cm (−4.8); son 2, 29.3 cm (−7.7); son 3, 31 cm (−6); son 4, 27.8 cm (−9.2); dau. 1, 33.7 cm (−0.3)
Sha., R.	F: 31.5 cm (−5.5); M: 31.5 cm (−2.5) son 1, 32.2 cm (−4.8); son 2, 31.5 cm (−5.5); son 3, 32.5 cm (−4.5)

g. Long "fibula" (fig. 17).

Gal., F.	F: 53 cm (+8); M: 47 cm (+6) son 1, 56 cm (+11); son 2, 49 cm (+4); dau. 1, 44 cm (+3); son 3, 53 cm (+8)
Gav., L.	F: 50 cm (+5); M: 44 cm (+3) dau. 1, 43 cm (+2); dau. 2, 44 cm (+3); dau. 3, 42.5 cm (+1.5); dau. 4, 44.5 cm (+3.5)
Scu., E.	F: 46 cm (+1); M: 41.5 cm (+0.5) son 1, 47 cm (+2); son 2, 46.5 cm (+1.5); son 3, 46.0 cm (+1.0); son 4, 45.1 cm (+0.1)

h. Short "fibula" (fig. 18).

Bro., F.	F: 42 cm (−3); M: 40 cm (−1) son 1, 44 cm (−1); dau. 1, 41 cm (±0)
Hoy., B.	F: 43 cm (−2); M: 40.4 cm (−0.6) dau. 1, 40 cm (−1); son 1, 43.2 cm (−1.8)
Tro., A.	F: 40.6 cm (−4.4); M: 41 cm (±0) (Ital.) son 1, 43.7 cm (−1.3); dau. 1, 40.2 cm (−0.8)
Scu., T.	F: 44.8 cm (−0.2); M: 38.4 cm (−2.6) dau. 1, 39.9 cm (−1.1); dau. 2, 40.1 cm (−0.9); dau. 3, 37.5 cm (−3.5)

Table 23 indicates that there are families (potential biotypes) in our population characterized by idiosyncrasies in respect to length of each of the segments of stature that we have been considering. Were selections in marriage made with reference to length of torso or leg it is plain that biotypes having these idiosyncrasies might quickly become established.

b. Particulate inheritance of segments of stature

If the segments of stature are inherited independently of each other, then in a child the length of torso may depend upon hereditary elements derived from one side of the house and length of fibula upon elements derived from the other side of the house. Is this expectation realized?

Data for answering this question fully are not available and yet there are indicators that this is so. For example, in the family of M. Wal. (fig. 11) the head and neck measure is in the father 1 cm above medium and in the mother 7.5 above; in the second son it is +2.9 cm, resembling more that of the father. The femur of the father is ± 0 ; of the mother -10.5 cm, in the second son it is -5 cm, resembling thus the *mother* in being decidedly short although not so extremely short as in her case.

Again, in the Cros. family head and neck is -3.5 cm in the father; -0.5 cm in the mother and +2.0 in the third daughter who thus resembles more her mother. Femur is -3.5 in the father; +0.5 in the mother and -2.0 in the third daughter who thus resembles more her father in this respect.

Again, in the J. Con. family, the head and neck is ± 0 in the father; -2.5 cm in the mother and +4.3 in the eldest daughter who is in this respect more like the father. The fibula is -0.5 in the father; +0.5 in the mother, and +3.8 in the daughter who is more like her mother in this segment.

The foregoing are merely examples of which many more could be gathered from table 23. They support strongly the conclusion that the segments of stature are to a certain extent separately inheritable.

A consequence of the independent inheritableness of the segments of stature is that one child may inherit the longest segments from both parental germ-plasms and the other child of the same fraternity the shortest segments. The first may be taller than either parent and the other shorter. An example follows:

A. Gui. has a stature of +9; his wife of +15.8; their eldest daughter of +28.0. Each segment of stature of this daughter save one resembles in length the longer segments of the corresponding parental segments—in three segments the resemblance is to the mother, in one to the father. Again, in the Str. family, the father has a stature of -2.8 cm; the mother of -1.0 but the daughter of +5.7 cm. In head and neck measures the father is -1.5 cm; the mother +2.8, and the daughter +4.4, resembling more the mother. In torso the father is +0.5 cm; the mother -5.0; the daughter +0.2 resembling closely the father. In this case the tall daughter seems to get her tallness by a summation of tall factors for two segments from opposite sides of the house.

Such cases might be multiplied greatly. They lead to the conclusion

that one reason why children of two tall parents are sometimes (though rarely) shorter than the parents is because of the chance of union of the short factors for different segments from opposite sides of the house. In general, if $a b C d$ be the factors carried by one parent, the capital letter representing a short segment, and $a B c d$ be the factors carried by the other parent, then the progeny may be $a B C d$ and thus have two shortening factors and be shorter than either parent.

3. *Inheritance of proportional lengths of stature segments*

Hitherto we have dealt with the absolute measures. In this section it is proposed to discuss the inheritance of *proportional* length; or the factors of stature contributed by the different segments when total stature is taken as 100.

a. Inheritance of proportional length of torso

First let us consider the case where both parents have relatively very long or long torsos.

TABLE 24

Mating: Long \times long torso, and condition of torso in the progeny.

Family	Parents		Children			
	F	M	1	2	3	4
Gut.	+2.9	+3.1	+0.4	+2.5		
Gol.	+1.9	+2.5	+1.7	+0.5	+1.3	+0.1
Pia.	+1.0	+1.4	+1.3	+2.1	+0.3	
Big.	+2.1	+1.1	+2.0	-1.2		
Lav.	+1.4	+1.8	± 0	-0.7		
Sha.	+5.2	+0.6	+3.6	-1.7		
Car.	+0.7	+2.4	+0.5	-1.9		
Wic.	+0.8	+0.8	-0.6			
Dav.	+0.6	+1.0	+1.3	-0.8	-0.9	+0.6

Table 24 shows that in the one mating where both parents have a very long torso the children (2) have likewise a torso above the average. When both parents have a torso which is 1 percent or more above the average there are about twice as many children with torso above the average length as below; and those above the average are far more extreme than those below the average. When merely one parent is "long" there is nearly an equal number of offspring above and below mediocrity.

Let us now compare the very short \times very short matings. There are 4 of them.

TABLE 25

Mating: Very short × very short torso, and condition of torso in the progeny.

Family	Parents		Children		
	F	M	1	2	3
Pro.	—5.5	—2.6	—1.5		
Rob.	—3.7	—3.0	—3.0	+1.3	—2.3
Smi.	—3.5	—2.7	—2.9	—2.2	
Dar.	—2.7	—2.7	—3.6		

Of 7 children from the class of mating of table 25 all but 1 have relatively short to very short torso.

We may now consider other matings into which "short" (or very short) enters with or without "long" torso.

While the number of individuals considered in table 26 is too small to make it worth while to calculate the elements of the distribution in

TABLE 26

Distribution of torso length in offspring of various matings as indicated at top of column.

Percentage filial deviation from normal	Column number and mating								
	1		2	3		4		5	
	S	VS	S	VL	S	L	VS	L	S
	× VS	× S	× S	× S	× VL	× VS	× L	× S	× L
+3.0 to +2.6									1
+2.5 to +2.1			1						
+2.0 to +1.6	2		2					3	
+1.5 to +1.1			1	1		1		1	
+1.0 to +0.6	3		2	1		1		1	
+0.5 to +0.1			7			3		5	
±0.0 to -0.4	2		9					10	
-0.5 to -0.9	4		8	4		4		8	
-1.0 to -1.4	3		14			4		13	
-1.5 to -1.9	6		11	1		4		7	
-2.0 to -2.4	5		22	2		3		4	
-2.5 to -2.9	2		5			3		1	
-3.0 to -3.4	2		9			2		1	
-3.5 to -3.9			4	1		2		2	
-4.0 to -4.4	1		3						
-4.5 to -4.9			1						
-5.0 to -5.4									
-5.5 to -5.9	1								

each column, it is obvious by inspection that: (a) The offspring of short \times very short have the greatest variability and extend their range in the direction of shortness more than any other mating. The progeny of short \times short show a greater tendency to concentrate—a smaller variability. Long \times short has a mode not far from 0 but clearly nega-

TABLE 27

Distribution of proportional torso length in offspring of matings in which one parent has a medium torso.

Percentage filial deviation from normal	Column number and mating				
	1	2	3	4	5
	M \times M	M \times S S \times M	M \times VS VS \times M	M \times L L \times M	VL \times M M \times VL
+5.0 to +4.6		1			
+4.5 to +4.1					
+4.0 to +3.6					
+3.5 to +3.1				2	
+3.0 to +2.6				1	
+2.5 to +2.1		1			1
+2.0 to +1.6		1		2	1
+1.5 to +1.1		1		5	1
+1.0 to +0.6		7		3	1
+0.5 to +0.1	2	5	7	1	1
± 0.0 to -0.4	2	13	3	3	1
-0.5 to -0.9	2	12	1	3	
-1.0 to -1.4	3	10	4	7	2
-1.5 to -1.9	2	14	2	4	2
-2.0 to -2.4		6	2		1
-2.5 to -2.9		5	1	1	
-3.0 to -3.4	1	1		3	
-3.5 to -3.9		1			
-4.0 to -4.4			1		1
-4.5 to -4.9					
-5.0 to -5.4					
-5.5 to -5.9	1				

tive. In the short \times very short mating (col. 1) two of the shortest individuals are from a single mating (Sch.: -4.0×-0.6).

It will be noted that all matings between long and short (cols. 3, 4 and 5) yield many more short than long torso in the progeny in the proportion of 76 below to 18 above the average, or 4 : 1. This is, again, evidence of dominant factors in short torso.

Finally table 27 shows the distribution of progeny when one medium parent enters into the combination.

In table 27 the progeny of medium \times short (or very short) mating averages relatively shorter than matings medium \times long (or very long). It is remarkable, and probably due merely to insufficient numbers, that the progeny of two parents both with medium torso should have pre-vaillingly relatively short torso. I cannot help entertaining a doubt as to the correctness of the two entries below —1.9 percent in the first column.

Summary. There is a clear evidence from table 26 of the dominance of one or more shortening factors in torso. Progeny of mating long (or very long) by short are in the proportion of 4 below mediocrity to 1 above. Short \times short torso yields about 12 percent above mediocre torso. Medium \times medium is very variable. The shortening factor in torso is, however, obviously not a single one.

b. Inheritance of proportional length of fibula

We will here consider first the distribution of progeny of similar matings (columns 1-5, table 28), then of matings between extremes (columns 6, 7) and finally of extremes with mediocrity (columns 8, 9).

First we note, in table 28, the reduction in the proportion of the fibula in the progeny *pari passu* with the reduction in the parental proportion. In the case of the long \times long mating 23 percent of the progeny are at or below mediocrity. In the case of the short \times short mating 45 percent of the progeny are above mediocrity. Here again the short condition clearly carries more allelomorphs than the long condition does. In the case of the medium \times medium mating the average of the progeny lies close to mediocrity. The commonest condition is, indeed, close to the medium but there are more cases outside the range of "medium" than inside that range. Also the number of cases above the average is about the same as the number below. When short is mated to long (or very long) most of the progeny is below mediocrity (60 to 70 percent). The mating medium \times short yields a great majority, about 75 percent, at or below the average; the mating medium \times long yields about half above the average. There seems to be a slight evidence of a segregation into short and long again, as well as medium.

Some of the short \times short matings yield a progeny of whom all have a relatively short fibula. Out of 8 matings that afford 2 or more children 3 yielded only offspring below average height and in two of these cases all offspring were "short" (i. e., —0.5 or shorter). There is a suggestion here that some of these parents were homozygous for short.

TABLE 28

Distribution of proportional "fibula" length in offspring of various matings.

Percentage filial deviation from normal	Column number and mating								
	1	2	3	4	5	6	7	8	9
	VL × VL	VL × L	L × L	S × S	M × M	S × VL	S × L	M × S	M × L
+4.0 to +3.6	2						2		
+3.5 to +3.1			1						
+3.0 to +2.6		1	3						
+2.5 to +2.1		2	2	1	2		1		2
+2.0 to +1.6	1	3	10	1	2		1		2
+1.5 to +1.1	1	0	8	1	3	0	3	3	8
+1.0 to +0.6		6	9	4	13	1	6	7	8
+0.5 to +0.1		2	10	4	19	2	7	12	15
±0.0 to ±0.4	2	1	5	3	12	5	3	27	21
-0.5 to -0.9		1	7	4	12	1	8	21	11
-1.0 to -1.4			1	2	5		18	21	6
-1.5 to -1.9				3	2	1	1	3	1
-2.0 to -2.4				1			1	2	
-2.5 to -2.9								0	
-3.0 to -3.4								1	

Of 20 long × long matings yielding 2 or more children 13 had no fibulas below the average proportions. In some families (Ford, 2; Conklin, 2; Shakeshaft, 3; Gerard, 4; Parisi, 4; Roselle, 3; Cozetti, 2) all offspring had "long" or "very long" fibulas. The Shakeshaft family is one of the most interesting in this regard. Father, +2.3 percent; mother, +1.0 percent; children: +1.8, +2.8, +3.0 respectively. The greater uniformity of the progeny of tall parents as compared with short indicates the factors that determine tallness are mainly recessive ones.

c. Inheritance of the proportional length of head and neck

This subject may be best introduced by a table giving the distribution of the progeny in all matings (table 29).

It is obvious that the length of head and neck is made up of many independently variable elements. The greatest variability arises from the combination of the germ-cells of two "short" parents and of two "long" ones, and least from two medium parents. Indeed, the offspring of two medium parents are closely massed around medium length, which indicates that "medium" is here not a typically heterozygous condition. Long × medium is heterozygous and has a rather high variability while short × medium, and long × short have a lower variability than either

TABLE 29

Distribution of deviations from average proportion of head and neck in the offspring of various matings.

Percentage filial deviation from normal	Column number and mating												
	1	2	3	4	5	6	7	8	9	10	11	12	13
	VL X VL	VL X L	VL X M	VL X S	L X L	L X M	L X S	L X VS	M X M	M X S	M X VS	S X S	S X VS
+5.8	11					1							
5.3	10				1								
4.8	9												
4.3	8		2										
3.8	7	1	1		1		1			1		2	
3.3	6	1	1	1	4	4				2		1	
2.8	5		2	1	3	6			2	1			
2.3	4	1	5	2	1	8	3		2	1		2	
1.8	3		2	2	10	14	5	1	3	8			1
1.3	2		1		8	14	2		3	2	1	2	
0.8	1		2		7	24	9		9	7	2		
0.3	0		5	1	13	16	2	1	10	15	1	6	1
-0.2	1		3	2	7	14	5	1	8	8	2	10	1
-0.7	2			1	1	8	5		3	10		4	1
-1.2	3				2	1	4		1	3		2	
-1.7	4						1	1	1	1			1
-2.2	5				2	1	1	2				1	2
-2.7	6		1			1				1			
-3.2	7								1	1			
-3.8	8							*					1†
σ					1.422	1.367	1.302		1.129	1.318		1.422	

*One case at -6.2 is omitted. †One case at -7.9 (probably erroneous or pathological).

short \times short, or long \times long. The results indicate that head and neck length depends upon a complex of factors which require further analysis.

V. SUMMARY

It appears that the inheritance of proportional length of the segments of stature is as evident as the inheritance of absolute differences. Here, too, it is obvious that the proportional shortness of any segment depends on more than one shortening factor—just how many cannot be said. Short \times short gives practically always a more variable progeny than long \times long, indicating that there are fewer factors in the germ-plasm of tall than of short parents. Medium stature is often found in the progeny of tall \times short; but there is a very numerous medium biotype which tends to breed true; so that the medium \times medium mating is not always characterized by excessive variability.

D. STATURE IN SPECIAL CLASSES

I. INFANTS

Infantile measures are difficult to obtain with accuracy because of the constant activity of the infant. Through the kind coöperation of Dr. FISHBERG I was permitted to measure 12 infants 1 to 9 days after birth at the JEWISH MATERNITY HOSPITAL, New York City. The total length (vertex to sole) varied from 47 to 52 cm.

The proportions found are given in table 30.

TABLE 30

Proportional length of the four segments of stature in 12 Jewish infants, 1—9 days old.

	1	2	3	4	5	6	7	8	9	10	11	12	Average
Vertex to sternum	22	21	24	21	20	25	24	22	23	19	22	20	21.9
Torso	46	44	46	46	48	44	48	50	46	50	49	47	47.0
Femur	12	14	10	12	10	13	11	9	11	14	10	11	11.4
Fibula	20	21	20	21	22	18	17	19	20	17	19	22	19.7

Comparing with our standard adult proportions (respectively, 18, 35, 21, 26) we see that the length of head and neck of infants is relatively great, that of torso is great, that of femur is only about relatively half of the adult and that of the fibula is short.

II. NEGROES

If the different anthropological "races" show a difference in proportions of the partial stature, that is evidence of the inheritance of the difference. On the occasion of a visit to Lexington, Kentucky, I was permitted to measure, through the courtesy of the superintendent of the STATE HOSPITAL and the coöperation of his wards, 12 "negro" men and 7 "negro" women. The average stature of the 12 negroes, eight of whom were probably of full blood and the others $\frac{1}{4}$ white, was 166.75 cm; but this included one dwarfish man of a stature of 150 cm. Omitting him the average stature of the male group is 168.3 cm which is about 5 cm smaller than the number used in this paper as the average stature of a white population. The stature found for conscript negroes and mulattoes by BAXTER (1875) in the U. S. was 169.3 cm. The average of the women measured by me was 157.8 cm which was about 2 cm shorter than our standard (160 cm).

The fibula in every case exceeded our standard of 26 percent of the entire stature and varied from 26.8 to 28.7 percent. The femur was slightly longer than the average. The torso was almost invariably shorter and sometimes very much shorter than our standard of 35 per-

cent. Thus it ranged from 29.2 to 33.1 and in one case to 35.5 percent. The relatively longer fibula and short torso are anthropoid characters. The head and neck of the negroes is generally in excess of the standard,

TABLE 31

Giving for each of 19 negroes, sex, age, total stature and, for each of the segments of stature, absolute length (in centimeters), percentage of stature, also deviation from absolute average length and deviation from average percentage of stature.

Sex	Stature	Head and neck %	Torso %	Femur %	Fibula %
♂	166.4	32.8 19.7	50.6 30.4	38.6 23.2	44.4 26.7
	-6.6	+0.8 (+1.7)	-8.4 (-4.6)	+1.6 (+2.2)	-0.6 (+0.7)
♂	171.7	32.8 19.0	54.2 31.5	38.5 22.6	46.2 26.9
	-1.3	+0.8 (+1.0)	-4.8 (-3.5)	+1.5 (+1.6)	+1.2 (+0.9)
♂	170.3	35.3 20.7	49.6 29.2	37.9 22.2	47.5 27.9
	-2.7	+3.3 (+2.7)	-9.4 (-5.8)	+0.9 (+1.2)	+2.5 (+1.9)
♂	168	30.7 18.3	52.1 31.0	38.0 22.6	47.2 28.1
	-5	-1.3 (+0.3)	-6.9 (-4.0)	+1 (+1.6)	+2.2 (+2.1)
♂	150.1	27.4 18.3	53.3 35.5	29.2 19.4	40.2 26.8
	-22.9	-4.6 (+0.3)	-5.7 (+0.5)	-7.8 (-1.6)	-4.8 (+0.8)
♂	172.7	32.1 18.5	54.3 31.5	37.6 21.7	48.7 28.3
	-0.3	+0.1 (+0.5)	-4.7 (-3.5)	+0.6 (+0.7)	+3.7 (+2.3)
♂	168.9	32.2 19.1	54.8 32.5	34.9 20.6	47.0 27.8
	-4.1	+0.2 (+1.1)	-4.2 (-2.5)	-2.1 (-0.4)	+2.0 (+1.8)
♂	169.7	33.7 19.8	51.6 30.5	38.1 22.4	46.3 27.3
	-3.3	+1.7 (+1.8)	-7.4 (-4.5)	+1.1 (+1.4)	+1.3 (+1.3)
♂	165.5	32.9 19.9	50.8 30.7	36.0 21.7	45.8 27.7
	-7.5	+0.9 (+1.9)	-8.2 (-4.3)	-1.0 (+0.7)	+0.8 (+1.7)
♂	174.7	28.5 16.3	55.0 31.5	41.0 23.5	50.2 28.7
	+1.7	-3.5 (-1.7)	-4.0 (-3.5)	+4.0 (+2.5)	+5.2 (+2.7)
♂	161.8	28.1 17.3	53.7 33.2	35.0 21.7	45.0 27.8
	-11.2	-3.9 (-0.7)	-5.3 (-1.8)	-2.0 (+0.7)	±0 (+1.8)
♂	161.2	23.8 14.7	53.9 33.5	38.2 23.7	45.3* 28.1
	-11.8	-8.2 (-3.3)	-5.1 (-1.5)	+1.2 (+2.7)	+0.3 (+2.1)
♀	163.7	31.2 19.0	52.8 32.3	34.5 21.1	45.2 27.6
	+3.7	+2.2 (+1.0)	-3.2 (-2.7)	+0.5 (+0.1)	+4.2 (+1.6)
♀	162.7	29.7 18.2	52.0 32.0	35.0 21.5	46.0 28.3
	+2.7	+0.7 (+0.2)	-4.0 (-3.0)	+1.0 (+0.5)	+5.0 (+2.3)
♀	157.8	30.2 19.1	52.8 33.5	30.8 19.5	44.0 27.9
	-2.2	+1.2 (+1.1)	-3.2 (-1.5)	-3.2 (-1.5)	+3.0 (+1.9)
♀	157.2	31.0 19.7	52.0 33.1	30.2 19.2	44.0 28.0
	-2.8	+2.0 (+1.7)	-4.0 (-1.9)	-3.8 (-1.8)	+3.0 (+2.0)
♀	156.3	27.8 17.8	51.7 33.1	33.1 21.2	43.7 27.9
	-3.7	-1.2 (-0.2)	-4.3 (-1.9)	-0.9 (+0.2)	+2.7 (+1.9)
♀	156.2	31.5 20.1	49.8 31.9	31.9 20.5	43.0 27.5
	-3.8	+2.5 (+2.1)	-6.2 (-3.1)	-2.1 (-0.5)	+2.0 (+1.5)
♀	151	30.2 20.0	48 31.7	30.3 20.1	42.5 28.2
	-9	+1.2 (+2.0)	-8.0 (-3.3)	-3.7 (-0.9)	+1.5 (+2.2)

except in the case of 2 men and 1 woman (who were probably not of full blood) and of an idiot with small cranium. This long head and neck is an infantile feature.

III. INDIANS

In September, 1916, I measured 11 "Indians" at the GOVERNMENTAL SCHOOL FOR INDIANS at Carlisle, Pennsylvania. Of these 9 were said to be full blood (table 32). All but two were under the average stature for males adopted in this paper. The head and neck was long, torso short and fibula slightly above the average, the "femur" being correspondingly short. In these respects the Indians measured, as compared with our standard, show a deviation toward the infantile type—a result quite unanticipated by me.

IV. CRETINS

For comparison I introduce (table 33) measurements taken on some cretins (5 females and 2 males) at Randall's Island—these all untreated with thyro-iodine. Their deficiency in stature varied from 64 to 25 cm. In all cases the head and neck were above the average (from 2 to 6 percent). In only one case is the proportional length of torso shorter than the average. In all the femur is abnormally short (3.0 to 5.6 percent below the average). On the other hand the proportions of the fibula vary about the average. Long head and neck and short femur are the striking peculiarities; they are infantile conditions.

V. DWARFS AND HEREDITY OF DWARFISM

While short stature is a clear racial character, there are cases of extremely short stature which are clearly pathological or teratological. Of the so-called dwarf races, the Akka Negrilloes of Central Africa have a height of about 138 cm (male stature) and the Negritos of the Philippines of about 147 cm. But a number of adult dwarfs among the whites measuring under 100 cm in stature are known. Such dwarfs are of two principal types, achondroplastic and ateliotic—the former having short legs with long trunk, the latter normal proportions but small size (fig. 19). While achondroplasia is probably due to improper internal secretions, the cause of ateliosis is more uncertain. Heredity of these two types has been considered by RISCHBETH and BARRINGTON (1912) without reaching any conclusion other than that the abnormal heights tend to recur in families.

TABLE 32

Giving for 11 Indians, at Carlisle Indian School, name, sex, age, stature and, for each of the segments of stature, absolute length (in centimeters), percentage of stature, also deviation from absolute average length and deviation from average percentage of stature.

Reference	Sex	Age	Stature	Head and neck	Torso	Femur	Fibula	Tribe
Hampton Tho.	♂	24	166.6 -6.4	35.0 +3.0 (21.0 +3.0)	54.0 -5.0 (32.4 -2.6)	35.5 -1.5 (21.3 +0.3)	42.1 -2.9 (25.3 -0.7)	Choctaw, Oklahoma
Jno. Cha.	♂	23	165.5 -7.5	32.4 +0.4 (19.6 +1.6)	55.0 -4.0 (33.2 -1.8)	34.4 -2.6 (20.8 -0.2)	43.7 -1.3 (26.4 +0.4)	Choctaw, New Mexico
Joe Day	♂	21	166.6 -6.4	32.4 +0.4 (19.4 +1.4)	58.4 -0.6 (35.1 +0.1)	32.8 -4.2 (19.7 -1.3)	43.0 -2.0 (25.8 -0.2)	Choctaw, New Mexico
David Was.	♂	22	166.8 -6.2	33.7 +1.7 (20.2 +2.2)	55.5 -3.5 (33.3 -1.7)	34.6 -2.4 (20.7 -0.3)	43.0 -2.0 (25.8 -0.2)	Creek, Oklahoma
Alac Enc.	♂	18	174.0 +1.0	31.9 -0.1 (18.3 +0.3)	57.2 -1.8 (32.9 -2.1)	38.7 +1.7 (22.2 +1.2)	46.2 +1.2 (26.6 +0.6)	Potowatan, Oklahoma
Hobson Tup.	♂	18	179.5 +6.5	34.2 +2.2 (19.1 +1.1)	57.5 -1.5 (32.0 -3.0)	40.3 +3.3 (22.5 +1.5)	47.5 +2.5 (26.4 +0.4)	Choctaw, Oklahoma
Ellian Bru.	♂	17	162.6 -10.4	32.7 +0.7 (20.1 +2.1)	53.3 -5.7 (32.8 -2.2)	35.6 -1.4 (21.9 +0.9)	41.0 -4.0 (25.2 -0.8)	Creek, Oklahoma
Sampson Ben.	♂	21	171.2 -1.8	33.3 +1.3 (19.4 +1.4)	58.7 -0.3 (34.3 -0.7)	34.2 -2.8 (20.0 -1.0)	45.0 ±0 (26.3 +0.3)	Choctaw, Oklahoma
Thomas Mon.	♂	20	160.0 -13.0	32.1 +0.1 (20.1 +2.1)	54.0 -5.0 (33.8 -1.2)	31.9 -5.1 (19.8 -1.2)	42.0 -3.0 (26.3 +0.3)	Pueblo, New Mexico
Frank Ant.	♂	17	168.0 -5.0	32.2 +0.2 (19.2 +1.2)	60.0 +1.0 (35.7 +0.7)	34.7 -2.3 (20.6 -0.4)	41.1 -3.9 (24.5 -1.5)	Chippewa, ¾ blood, Wisconsin
Joseph Pop.	♂	17	172.3 -0.7	33.3 +1.3 (19.3 +1.3)	54.0 -5.0 (31.4 -3.6)	39.3 +2.3 (22.8 +1.8)	45.7 +0.7 (26.5 +0.5)	Chippewa, ½ blood, Minnesota



FIGURE 19.—Photograph of a group of dwarfs and midgets exhibited at Luna Park, Coney Island, 1915. From left to right, Irwin Emmer, Samuel Goldstein, Louis Comadori, Baron Magri, Addie Frank, Joseph Zaino, Helen L. Haskell, Elsie King, Joe Short, Nona Appleby, Helen Linoner, Patrick McGoff, George Laible, Annie Nelson (Mrs. George Laible). Photograph by CHAS. NESENHORN.

TABLE 33

Giving for each of 10 cretins, reference letters, sex, age, stature (absolute and by deviation from average) and, for each of the segments of stature, absolute length (in centimeters), percentage of stature, also deviation from absolute average length and deviation from average percentage of stature.

Reference	Sex	Age	Stature	Head and neck	Torso	Femur	Fibula	%
Rose Sor.	♀	14	118.4 -41.6	24.7 -4.3 (+2.8)	42.2 -13.8 (+0.7)	21.9 -12.1 (-2.5)	29.6 -11.4 (-1.0)	18.5 (-2.5)
Josephine Red.	♀	27	133.1 -26.9	27.3 -1.7 (+2.6)	46.7 -9.3 (+0.1)	21.1 -12.9 (-5.2)	38.0 -3.0 (+2.5)	15.8 (-5.2)
Sadie Gro.	♀	15	132.9 -27.1	26.8 -2.2 (+2.2)	45.7 -9.3 (+0.2)	21.4 -12.6 (-4.9)	38.0 -3.0 (+2.5)	16.1 (-4.9)
Hannah Sil.	♀	23	124.7 -35.3	24.2 -4.8 (+1.3)	47.4 -8.6 (+3.1)	22.4 -11.6 (-3.0)	30.7 -10.3 (-1.4)	18.0 (-3.0)
Mary Don.	♀	21	134.0 -26.0	27.3 -1.7 (+2.4)	46.9 -9.1 (±0)	20.7 -13.3 (-5.6)	39.1 -1.9 (+3.2)	15.4 (-5.6)
Katie Zac.	♀	33	103.6 -56.4	22.5 -6.5 (+3.7)	39.0 -17.0 (+2.7)	18.5 -15.5 (-3.2)	23.6 -17.4 (-3.2)	17.8 (-3.2)
Frances Pen.	♀	15	113.8 -46.2	23.2 -5.8 (+2.4)	42.0 -14.0 (+2.0)	20.3 -13.7 (-3.2)	28.3 -12.7 (-1.2)	17.8 (-3.2)
Becky Kle.	♀	14½	115.7 -44.3	23.5 -5.5 (+2.3)	42.5 -13.5 (+1.8)	21.0 -13.0 (-2.9)	28.7 -12.3 (-1.2)	18.1 (-2.9)
Bennie Lon.	♂	37	109.2 -63.8	26.5 -5.5 (+6.3)	36.0 -23.0 (-2.0)	19.7 -17.3 (-3.0)	27.0 -18.0 (-1.3)	18.0 (-3.0)
Jimmie Mur.	♂	19	128.7 -44.3	24.7 -7.3 (+1.2)	49.0 -10.0 (+3.1)	21.3 -15.7 (-4.5)	33.7 -11.3 (+0.2)	16.5 (-4.5)

1. *Achondroplasia*

An examination of the pedigrees of achondroplastic dwarfs in the *Treasury of Human Inheritance* shows a few families in which the abnormality passed through several generations without a break. Thus in No. 608 there are shown 5 generations of "little people" in direct line. In the first generations the progenitors are said to be small but not so small as the later descendants. In the third generation is an achondroplastic dwarf. He had, by a wife of normal size, 11 children of whom 4 died in infancy. Of the remaining 7, 5 are large and 2 are small. One of the large ones married a normal man and had 5 children of whom one was an achondroplastic dwarf and died at the age of 3 years. One of the small ones married an ateliotic dwarf and is said to have had an ateliotic son only about 60 cm tall. The other small one had, by a normal-sized man, a son and a daughter who died in infancy and also a daughter who is achondroplastic and about the height of her uals, all males, and about 132 cm tall.

The *Treasury* includes a number of cases of direct heredity through 3 generations. Some of these are briefly described here.

No. 613. A very small man, not over 150 cm tall and ateliotic, had several normal children and one daughter, achondroplastic and 115 cm tall. She had a daughter in turn and later a son, both achondroplastic like the mother. A third child was not achondroplastic.

No. 619. In three generations there are six achondroplastic individuals, all males, and about 132.0 cm tall.

No. 622. An achondroplastic man about 105 cm tall had two normal children, an achondroplastic daughter who died at $7\frac{1}{2}$ years and an achondroplastic son 110 cm tall who in turn has 3 young children including one son who at 6 years shows the same anomalies as his father, height, 81.5 cm.

No. 623. A man and his son are both achondroplastic, about 135 cm tall. By a normal woman the latter has a son and two daughters. One of the latter is normal in stature (165 cm) but the other daughter, aged 27 years, is 118 cm tall with short legs; while the son, at 30 years, is 121 cm tall and short-legged.

No. 625. A dwarf had by a normal-sized woman "numerous" children. Two sons and a daughter are dwarfs. One of the sons is 160 cm tall with short appendages; he married a big woman who bore him 12 children besides having had 3 abortions. Four of the 12 are dead and 3 of the remaining 8 are achondroplastic like their father. They are

all girls and at 23, 21, and 19 years measure 95, 110, and 106 cm respectively. The father's brother, much smaller than the father, also had numerous children, mostly dwarfs.

No. 664. A "dwarf" had 8 children, of whom 6 were dwarfs, all, so far as known, achondroplastic. One such (123 cm tall) by a normal man had an achondroplastic daughter.

A number of other cases could be cited of achondroplastic dwarfism in parent and child.

On the other hand it is by no means true that one of the parents of an achondroplastic child is necessarily achondroplastic. Thus a girl at 26, 99 cm tall, and her brother, 25 years, 111 cm tall, had normal trunks but short legs. Both the father and the mother are normal and so are all other known close relatives, including 5 sibs.

Sometimes a generation is skipped. Thus in No. 620 a girl of ten is extremely achondroplastic, "suffering from typical rachitis." Her mother is normal and married to a big man. This mother's father was a dwarf with much curved short limbs.

Again, No. 616, a boy of 5½ years is only 85 cm tall and has relatively short appendages. His father is 166 cm tall and his mother is of medium height and healthy. This mother's mother was very small, with short hands and feet.

This skipping of generations (of which there are not many cases) would speak against the view that the achondroplastic dwarfism is a simple dominant trait. Also in *most* of the pedigrees the achondroplastic dwarf appears as the only case in the family. Perhaps we may conclude, with PLATE (1913, pp. 349-353), that "in achondroplasy there is a dominant (growth-inhibiting) factor, but that its full expression is often interfered with by other growth-stimulating, or by cancelling or antagonistic, factors."

2. *Ateliosis*

The longest pedigrees of ateliosis in the direct line extend through 3 generations. There are two of these. No. 731 begins with a man who was only 120 cm tall and was exhibited in shows as a dwarf for 21 years. He had a tall brother. The dwarf married a woman of normal stature and had 2 children. The first, a girl, was small "like a doll" at birth. She grew until she was 13 or 14. She wears gloves of 00 size and shoes of "children's sevens." She is 129.5 cm tall. Her brother was of the usual size at birth but grew slowly; at 38 years he is 132 cm tall. He married a normal-sized woman and had 7 children. Four of

them died when about 3 months old and all are said to have been dwarfs, but this is uncertain. Of the 3 living, 2 are well-developed girls; the one boy is a dwarf aged 10 and is 95 cm tall and a cryptorchid.

No. 695. A Piedmontese Italian man, strong but very small, about 110 to 120 cm tall, had 8 children (2 of whom died young). Of these one is ateliotic. At 33 he is 110 cm tall. He is sexually potent and, by a woman of normal height, has had 2 children and a miscarriage. The elder child is a girl who at birth was very small and at 22 months is behind other children in size although well-proportioned.

No. 747 is a remarkable family but the form of dwarfism is uncertain. We begin with an Italian couple of tall stature who had 5 children of whom all were tall but one. He was a dwarf, 113 cm tall and well-proportioned in all parts of his body. He married a normal woman and they had 9 children of whom 3 died in infancy; 5 of the remaining 6 were dwarfs. 1, ♀, was 113 cm tall and never married. 2, ♂, 135 cm tall, married twice; by his first wife he had 4 children of whom 3 died young and 1 survived to marry; by his second wife he had 4 sons of whom 1 died young, and the other 3, although young, are apparently dwarfs; one at 14 years is 94.5 cm tall; one at 9, 97 cm; one at 7, 91 cm. 3, ♂, only 130 cm tall, married a normal woman and had 5 children; one died young; one is normal; and the other 3 children, though young, are said to be dwarfs. 4, ♀, at 41 years is scarcely 98 cm tall; 5, ♀, is normal; 6, ♀, at 31 is 116 cm tall. The dwarfism in this case is regarded by RISCHBETH and BARRINGTON (1912) (on what ground they do not say) to be "scarcely ateliosis."

An extensive pedigree of ateliotic dwarfism is that of the Prinz and Jenal families of Samnauntal in the Tyrol. These families have repeatedly intermarried and two, at least, out of 3 fraternities containing ateliotics, are from intermarriages of these strains. As PEARSON suggests (*Treasury*, p. 501, footnote), "The pedigree seems to indicate that true dwarfism might be recessive in the stock ancestral to both Prinz and Jenal families."

I will add some special data on file at the EUGENICS RECORD OFFICE relating to dwarfs:

S. F. ♀, at 40 years is 97 cm tall; all of her children by a man 168 cm tall are apparently of normal size. She has a normal sister who, by a normal man, has two sons. The first at 21 years is 157 cm tall; the second at 15 years is of the size of an 11-year-old child (i. e., about 134 cm, instead of 165 cm). (E. R. O. 024-17.)

Peter W. T. was of normal stature and so were his father and mother.

He had, however, a sister, Cynthia, who was only 104 cm tall. She was of normal intelligence; she never married. Another sister, Lucretia, was 106.7 cm tall; but a third sister and the only brother were of normal height. Peter married a woman of normal stature, possibly related to him. There were 7 children of whom 2 were dwarfs. Of these, one, Emma, was only 78.7 cm tall, weighed 35 pounds and died, unmarried, at 49 years. The other, Addison, was so small that he was sought by P. T. Barnum, the showman. He died at the age of 53 years in an epileptic attack. One of the normal children, Daniel, has a grandson who, at 15 years, is undersized. In view of the fact that this family-complex lived almost under insular conditions the marriages were probably consanguineous in some degree. The inheritance resembles that of a recessive trait. (E. R. O. 15: 343.)

A feeble-minded man, about 168 cm, married a woman who was competent but a small dwarf. Of her 7 sibs one brother and one sister were each about 132 cm in height. The short sister had 3 children of normal size. The father of this fraternity had a height of 132 cm. The children of the first named pair numbered 6: 1, ♀, feeble-minded, measured about 150 cm; 2, ♀, was a little over 152 cm; 3, ♀, was 130 cm and had, out of 7 children, one who is only 132 cm high; 4, ♀, about 132 cm tall, had 2 daughters who are cretins, another who is a dwarf and has responded little to thyroid treatment, while 2 are normal. Nos. 5 and 6 were of medium stature. Here one or more shortening factors seem to be "inherited" as a dominant; at least there is an inherited tendency to defect in growth-promoting secretions.

What conclusion can be drawn from the foregoing pedigrees and others that are in the literature? It seems almost necessary to conclude from pedigrees in which the dwarfing tendency has been inherited in a direct line once for 5 generations and several times for 3 generations, that there is present an important *dominant* factor. That only one dominant factor is present in dwarfing cannot, of course, be said. In other cases the result looks as if a recessive factor was at the bottom of ateliosis though one cannot agree with WEINBERG (1912) that we have ever to do with a simple recessive. The offspring of two ateliotics are *usually* of full size at birth and some have developed into full-sized persons. I am inclined to conclude that in both ateliosis and achondroplasia there are multiple dominant (growth-inhibiting) factors—whose actions are also often obscured by opposing epigenetic growth factors, and which are probably of a different sort in ateliosis than in achondroplasia, for achondroplasia affects chiefly or exclusively the appendages.

VI. GIANTS AND HEREDITY IN GIANTISM

CUSHING (1912, pp. 158-170) records a case of a man who at 12 was 183 cm (6 ft) tall and is now, at 48 years, 185 cm (73 in.) tall despite extreme bowing of shoulders. His mother's father was a "giant"; his mother was of average build. He was one of 9 children; one sister of the propositus is large and closely resembles the patient. He married a large woman weighing 200 pounds.

"She had 3 pregnancies; the first, 10 years after marriage, resulted in a child too large to be born. A second child, a girl weighing 17 pounds at birth (1898), survives, and now at 11 years of age is 152 cm (5 ft) in height and weighs 100 pounds. The third, 'an enormous child,' died in its first year from unknown cause."

The case is interpreted as due to extraordinary hypophyseal activity of which there was an exacerbation between the fifteenth and twenty-fifth years.

Again (CUSHING 1912, p. 201), S. G., ♂, 20 years of age, of "high-strung and nervous" parentage, height 179 cm, has dyspituitarism. He has a brother about 193 cm tall and a father 189 cm; his father's father and two uncles are over 183 cm (6 ft).

Of tall families, the Howard family is one of the most interesting: Father, 193 cm (76 inches); mother, 184 cm (72.5 inches). She had 12 brothers and sisters over 183 cm (72 inches) tall. Children: Thomas, 193 cm (76 inches); James, 198 cm (78 in.); John, 214 cm (6 ft. 11½ in.); Elijah, 191 cm (6 ft. 3 in.); Matthew, 198 cm (78 in.); Eli, 199 cm (78.5 in.); Sarah, 188 cm (74 in.); Mary, 188 cm (74 in.); Daniel D., 191 cm (75 in.). In 1856 there were several grandchildren growing over 198 cm (6½ feet) tall. Descendants of the Howard family are now living at Lexington. I measured one who was 188 cm (6 ft. 4 in.) tall and several other men between that height and 183 cm (6 ft.), and two more over 182 cm (5 ft. 11 in.).

Another strikingly tall family is that of the Mac Queens of Queensdale, North Carolina (see MAC ELYEA 1916, from which I quote). The progenitor immigrant was Col. James Mac Queen, born on the Isle of Skye, Scotland, about 1760. "He was a man of superb physique and noble presence." His parents were Archibald Mac Queen and Flora Mac Donald, his wife. He married Ann Mac Rae, "above the medium height," and had 12 children of whom 11 grew to maturity.

1. Archibald "of the finest physical mold"
2. Flora
3. Katherine "far above the size of the average woman"

4. Sarah
5. Edmund "fully six feet in height"
6. Annabella "of tall, finely proportioned figure"
7. Neill "tall and slender"
8. John "tall, of erect and splendid physique, magnificent proportions"
9. James "not so tall as his brothers"
10. Maria "of medium height and stout"
11. Charity "tall and slender"

The foregoing account of the children of Col. James Mac Queen, though not quantitative, shows that, of the 9 children described, 7 were strikingly tall and two were "medium" or "not so tall." But it must be recalled that the author of the Mac Queen history lived in a community of strikingly tall persons, so that her idea of "medium" may have been above the standard adopted by this paper.

The tall Katherine (No. 3) married Col. Donald Mac Queen—"a man of gigantic physical proportions." They had several children who grew up:

1. Alexander (6 ft. 3 or 4 inches)
2. Nancy (6 ft.)
3. James (6 ft. 2 in.)
4. Flora "carried the typical stature and size of the family";
"of imposing presence" (5 ft. 11 in.)
5. Sallie (5 ft. 10 in.)
6. Margaret (5 ft. 10 in.)
7. Martin "tall" (6 ft. 4 in.)
8. Archibald "a man of splendid physique" (6 ft. 2 in.)*
9. Effie "a woman of remarkable height, measuring fully six feet" (5 ft. 10 in.)
10. John "exceedingly tall and oftentimes I have seen him bow his head in entering the door of a room" (6 ft. 5 in.)
11. Edmund (6 ft. 4 in.)
12. Katherine (5 ft. 11 in.)

(The heights in parenthesis were given me by two or three members of the family.)

Thus all of the children of the tall Katherine and Donald Mac Queen were tall or very tall. I measured a son of No. 5, Sallie; he (Alexander J.) was 187 cm (73.6 in.) tall; a son of his (Henry) was 185 cm (72.8 in.) tall and a son of the latter was 189 cm (74.4 in.) tall. In-

deed, all 3 sons of Sallie were over 6 feet, without shoes, and Henry's children (by a tall wife) are all tall or very tall.

John (No. 8), the son of Archibald and Flora, married a woman who "was above the medium height" and "her three sons grew up as giant monuments" (p. 177) being, 6 ft. 1 inch, 6 ft. 4 inches, and 5 ft. 11 inches, respectively. There are plenty of other examples of tall members of this interesting family of north Scotch origin.

Assuming that excessively tall stature is the result of excessive activity of the pituitary gland, then it seems necessary to conclude that peculiarities in the functioning of endocrine glands are influenced by genetic factors—have an inheritable basis.

In all the foregoing families when both parents are tall all of the children are tall; this indicates that the factors for tallness are mostly recessive—probably due to the absence of inhibition to prolonged growth.

E. SUMMARY OF CONCLUSIONS

1. One of the factors that determines variation in stature is probably the variation in age of onset of puberty.
2. Parents of similarly deviant stature have on the average less variable offspring than those of one short and one tall parent.
3. The offspring of two tall parents are less variable in stature than those of two short parents.
4. When both parents are "tall" or "very tall," and of tall stock, practically all the children are tall or very tall.
5. When both parents are "very short" or "short," and of short stock, all children are short or very short.
6. The hypothesis that is tested in this paper is: "short" parents may, and frequently do, carry germ-cells which lack the shortening factors, while in tall parents the gametes are more nearly homogeneous and all lack most of the shortening factors.
7. When the parents are much below the average in stature the offspring regress toward mediocrity; but when the parents are much above the average in stature there is no (or little) filial regression.
8. The least variable offspring are those of two tall parents; the most variable those of parents that are abmodal in opposite directions.
9. The progeny derived from matings of similars are less variable than those derived from matings of dissimilars—a result which indicates that parents of all classes are somewhat heterozygous.

10. Medium stature may appear in the progeny of a tall \times short mating, but the majority of persons of medium stature in this country belong to a medium biotype.

11. The truth of the hypothesis formulated in paragraph 6 seems to be established. Shortness is due to certain positive factors that inhibit growth of the various parts.

12. Persons of similar stature tend to marry each other; and extremes are more particular in this respect than those of medium statures.

13. While "growth-as-a-whole" factors are present, yet there is a large degree of independence in the variability of the four segments of stature, considered in this paper. Thus the correlations between supra-sternal and substernal segments is $.09 \pm .04$; between knee-to-pubic arch ("thigh") and knee-to-sole ("tibia") $.24 \pm .04$; between standing and sitting height $0.64 \pm .03$. This independence in variability of the segments of stature makes impossible any simple "Mendelian" laws of inheritance of stature as a whole.

14. Height of upper edge of symphysis pubis varies from 43.6 to 56.5 percent of stature. The ratio of trunk length to stature ranges from 35 to 25.5 percent of stature. The head and neck constitute about 17 percent of the stature.

15. A study of torso length shows that short \times medium matings yield offspring that fall, on the average, below mediocrity far more than the offspring of tall \times medium surpass mediocrity.

16. The parental category of medium torso seems to be so commonly heterozygous that the progeny of two parents with medium torso are exceptionally variable.

17. When both parents have short fibula about one-fifth of the progeny are at or above the mean stature; when both parents have long fibula none of the offspring are short. In respect to fibula, again, "short" carries the more variable gametes. Here, too, the offspring of two medium parents are exceptionally variable.

18. When both parents have short head and neck about 48 percent of the progeny are medium or above in length of this segment. When both parents have long head and neck about 10 percent of the progeny are medium or below in length of this segment. The offspring of short \times short (or very short) matings are more variable than those of long \times long (or very long) matings.

19. In general, parental short segments yield a progeny more variable in respect to the given segment than parental long segments; matings long \times short yield progeny with a relatively low variability and matings medium \times medium progeny with a relatively high variability.

20. In the segments of stature (as contrasted with stature as a whole) we approach a condition of relatively few factors for the character.

21. There are families (potential biotypes) in our population characterized by idiosyncrasies in length of each of the segments of stature.

22. There is evidence that the segments of stature are to a certain extent separately inheritable.

23. One reason why children of two tall parents are sometimes (though rarely) shorter than the parents is because of the chance of the union of the short factors for different segments from opposite sides of the house. In general, if *abCd* be the factors carried by one parent (the capital letter representing a short segment) and *aBcd* be the factors carried by the other parent, then the progeny may be *aBCd* and thus have two shortening factors and be shorter than either parent.

24. The inheritance of *proportional* length of the segments of stature is as evident as the inheritance of absolute differences. Here, too, it is obvious that proportional shortness of any segment depends on more than one shortening factor—just how many cannot be said.

25. The deviations from our standards of the stature segments of infants, negroes, Indians and cretins are similar. These deviations may be called infantile.

26. It is probable that in all forms of dwarfing there are multiple dominant inhibiting factors.

27. In the case of giants, when both parents are tall all of the children are tall; this indicates that the factors for tallness are mostly recessive—probably due to the absence of inhibitions to prolonged growth.

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VARIEGATION IN PLANTAGO

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INTRODUCTION

Plantago major, one of the commonest weeds in Europe and America, grows also almost everywhere in Japan, the form growing here being considered by our systematists to be a sub-species "*asiatica*". There are also many garden races of this species known here, of which some are now being used in breeding experiments in our Botanical Garden. Among others there is a variegated race of which figure 1 represents an adult plant, and figure 2 a number of young seedlings. In this variety parts without chlorophyll are at first nearly white but gradually become pale yellow. The variegated plants reveal themselves generally very soon after germination, because the cotyledons are usually variegated, but sometimes the cotyledons are entirely green and then their real nature can be discerned only after the formation of the first, second, or even the third foliage leaf. The variegated plants seemed at first to breed entirely true to type by self-fertilization, but later it was discovered that a few green plants are rarely produced from them. These green plants will be considered in a later section (see page 413).

F₁ GENERATION

In 1912 I hybridized one of these variegated plants with a self-colored green one, reciprocally. All F₁ plants made in both reciprocal ways were self green.

In *Mirabilis Jalapa*, according to CORRENS (1909, p. 303), the hybrid between a variegated and a green race is somewhat paler green than the original green plant, the green color being not perfectly dominant over the variegated condition. In *Plantago* I was unable to detect

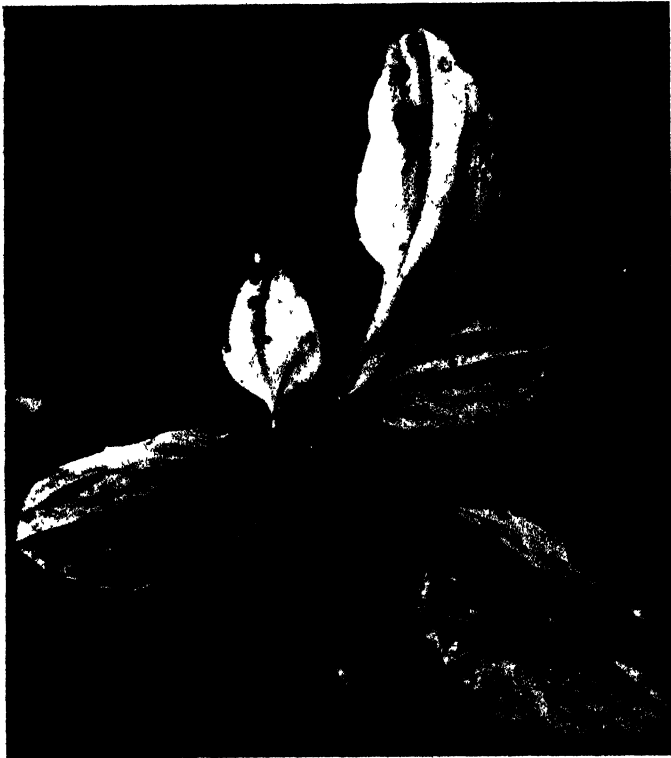


FIGURE 1.—An adult plant of variegated *Plantago*, seen from above. Natural size.

any appreciable difference between the pure green parent and the F_1 hybrids, in the intensity of their green color. HERIBERT-NILSSON (1912, p. 109), in his hybridization experiments with variegated and green plants in certain species of *Oenothera*, secured green hybrids, but on treatment of leaves of these hybrids by the well-known iodine method of SACHS he found that some parts of the leaves, being unable to produce an excess of carbohydrates, did not stain blue. He concluded rightly that in this case the variegation is *apparently* but not *really* a pure recessive character. I have made the same experiment on leaves of the F_1 hybrids of variegated and green *Plantago*. I plucked the leaves of

normal green plants as well as of F_1 hybrids in the evening of a bright summer day and treated them by the iodine method. Both kinds of leaves were stained intensely black and uniformly throughout their whole extent.

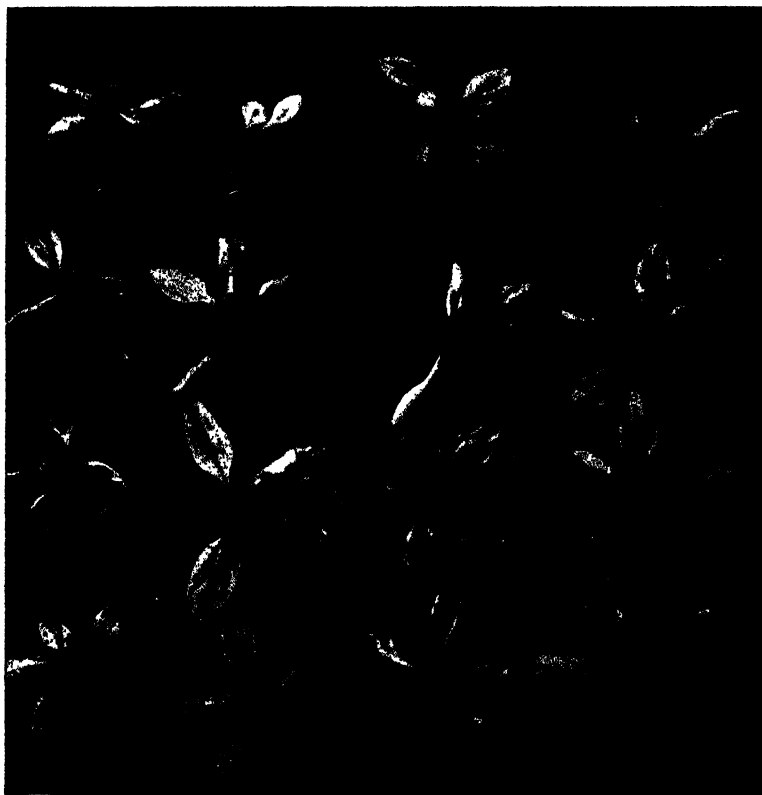


FIGURE 2.—Young seedlings of variegated *Plantago*, seen from above. Natural size.

Thus, neither in respect to the intensities of their green color nor concerning their mode of carbon assimilation is any difference to be detected between the green parent and the F_1 plants. We may conclude therefore that in *Plantago* the self-colored green is perfectly dominant over variegation.

F_2 GENERATION

The F_2 generation produced by the F_1 hybrids above described was found in 1913 to contain green and variegated plants in the ratios indicated in table 1.

TABLE I

F ₁ plant	F ₂ generation			
	Number of green	Number of variegated	Totals	Ratio of green to variegated
Green × variegated	1176	82	1258	14.957 : 1.043
Variegated × green	1753	118	1871	14.991 : 1.009
Totals	2929	200	3129	14.977 : 1.023

From table I we have 2929 green and 200 variegated, both together 3129; or we have 14.977 green and 1.023 variegated per 16, thus $\alpha = \pm 0.023$, while $E_M = \pm 0.047$.¹

Thus we see that in F₂ the hybrids segregate in the ratio 15 green to 1 variegated, indicating that we are dealing here with a case of so-called polymery, which has become a well known phenomenon since the important discovery of NILSSON-EHLE (1909). When my experiments were begun there had been no detailed studies of the successive generations of such hybrids, except the work of NILSSON-EHLE, just cited, and that of EAST (1911). I decided therefore to study these *Plantago* hybrids in some detail. Meanwhile in 1914 appeared an elaborate paper by SHULL (1914 a) on the duplicate genes determining the capsule-form of *Capsella bursa-pastoris*, but I have continued my study, since not only is the character involved in my investigation entirely different from those previously studied, but also, as SHULL has pointed out, there are in the literature very few cases of polymery adequately proven.

It will be noticed here that for studying the later generations the hybrid green ♀ × variegated ♂ has been used exclusively, but there is no doubt that the reciprocal hybrid will behave in exactly the same way as the one actually used in the present experiments.

F₃ GENERATION

Before passing further I will consider briefly what results should be expected in the F₃ generation. If, for instance, we denote two factors or genes for the self-colored green plants by *G* and *H*, respectively, we have the formula *GGHH* for green parents and *gghh* for the variegated

¹ α = deviation from the expectation; E_M = probable error of the mean = $\frac{0.6745 \times \text{standard deviation}}{\sqrt{\text{number of individuals}}}$, i. e., $\frac{T\sigma}{\sqrt{n}}$

ones. In F_1 we have therefore $GgHh$ and consequently in F_2 we should have the zygotes represented by the following genetical formulae²:

Class 1	Class 2	Class 3	Class 4
$GGHH$ (1)	$GgHh$ (4)	$ggHh$ (2)	$gghh$ (1)
$GgHH$ (2)		$Gghh$ (2)	
$GGHh$ (2)			
$GGhh$ (1)			
$ggHH$ (1)			

The Arabic numerals in parentheses denote the number of individuals having the indicated genotypic constitution.

Of these 16 individuals, belonging to four classes, the one in class 4 is variegated and recognizable as such in F_2 . I have already shown that the number of variegated plants actually secured in the F_2 approaches very nearly to this expectation (cf. table 1). The nature of plants belonging to the three other classes can be revealed only through their behavior in F_3 . Each of the individuals of class 1 (7 in every 16) are expected to breed true to greenness in F_3 , while those of class 2 and 3, each of them comprising 4 individuals in every 16, should yield green and variegated plants in the ratios of 15 : 1 and 3 : 1 respectively.

To ascertain whether this expectation is fulfilled 80 plants belonging to the F_2 generation were selected at random and grown to maturity. Seeds from each of these, produced by self-fertilization, were sown in 1914, and seedlings examined in 1914 and 1915. It was found that of these 80 plants, 37 produced exclusively green offspring.³

The number of seedlings arising from each of these parents was not specially counted, but generally several hundreds or sometimes even more than one thousand were raised from each. Of the remaining 43 F_2 plants, 25 were found to segregate in the ratio 15 green to 1 variegated, and 18 in the ratio 3 to 1, as shown in tables 2 and 3 respectively.

In table 2 we have thus 12855 green plants and 827 variegated, or 15.033 and 0.967 in 16; therefore we have $\alpha = \pm 0.033$, while we have $E_M = \pm 0.022$, the deviation being 1.5 times the probable error of the mean.

² Only the designation of the genes and their number in each formula are here taken into consideration, but not their origin from the male or the female side respectively, it being taken for granted that both $GHgh$ and $ghGH$ are appropriately represented by $GgHh$.

³ The pedigree Nos. of these 37 plants are: 3, 4, 5, 6, 9, 10, 17, 20, 21, 22, 28, 31, 32, 34, 40, 43, 46, 47, 49, 50, 53, 54, 55, 57, 59, 60, 61, 62, 63, 64, 66, 68, 78, 79, 82, 83, 86. .

TABLE 2

Pedigree No. of F ₂ plants	Number of green	Number of variegated	Totals	Ratio of green to variegated
1	1448	80	1528	15.162 : 0.838
2	720	37	757	15.218 : 0.782
11	608	37	645	15.082 : 0.918
15	731	58	789	14.824 : 1.176
16	405	38	443	14.628 : 1.372
18	823	48	871	15.118 : 0.882
24	706	55	761	14.844 : 1.156
25	599	37	636	15.069 : 0.931
27	377	24	401	15.042 : 0.958
30	407	27	434	15.005 : 0.995
35	166	7	173	15.353 : 0.647
38	482	41	523	14.746 : 1.254
42	673	35	708	15.209 : 0.791
44	458	18	476	15.395 : 0.605
45	528	31	559	15.113 : 0.887
48	236	19	255	14.808 : 1.192
52	479	27	506	15.146 : 0.854
56	944	56	1000	15.104 : 0.896
72	119	14	133	14.316 : 1.684
73	52	6	58	14.345 : 1.655
74	99	12	111	14.270 : 1.730
76	260	15	275	15.127 : 0.873
80	655	55	710	14.761 : 1.239
81	639	41	680	15.034 : 0.966
85	241	9	250	15.424 : 0.576
Totals	12855	827	13682	15.033 : 0.967

In table 3 we have 6002 green and 1819 variegated plants, or 3.070 and 0.930 in 4; therefore we have $a = \pm 0.070$, while $E_M = \pm 0.013$. The deviation is thus a little more than 5 times the probable error. This very small excess would not mean much, especially as the progenies fulfill the expectation very well in the next generation (cf. table 5 B, second part). The following fact may be noticed here, however. Our preliminary examination of variegated plants in 1912 and 1913 revealed the fact that their nature may generally be determined by the inspection of the cotyledons, which were at that time believed to be always variegated; so in 1914 and partly in 1915, seedlings were distinguished into green and variegated simply by the color of their cotyledons; tables 2 and 3 are the results of such countings. In the summer of 1915, however, it was discovered that sometimes, though not frequently, varie-

TABLE 3

Pedigree No. of F_2 plants	F_3 generation			
	Number of green	Number of variegated	Totals	Ratio of green to variegated
7	861	227	1088	3.165:0.835
8	627	210	837	2.996:1.004
12	613	189	802	3.057:0.943
13	700	214	914	3.063:0.937
14	329	121	450	2.925:1.075
19	241	111	352	2.739:1.261
23	425	90	515	3.301:0.699
26	311	120	431	2.886:1.114
33	467	134	601	3.108:0.892
39	201	42	243	3.309:0.691
41	153	39	192	3.187:0.813
58	130	37	167	3.114:0.886
65	178	50	228	3.123:0.877
67	53	12	65	3.262:0.738
69	10	6	16	2.500:1.500
70	25	10	35	2.857:1.143
71	312	98	410	3.044:0.956
77	366	109	475	3.082:0.918
Totals	6002	1819	7821	3.070:0.930

gated plants have green cotyledons, so that the true nature of such plants may be determined only after the development of the first, the second, or even the third foliage leaf. Since the summer of 1915 countings of green and variegated plants have not been made before the formation of their third leaf; tables 4, 5, and 8 are the results of such countings. The excess of the deviation over five times the probable error of the mean just above noticed is due to the insufficiency of the number of variegated plants, and this is in its turn due very probably to the fact that some variegated plants with green cotyledons were entered as green plants.

The 80 green F_2 plants selected at random were thus found to be composed of 37 individuals which breed true in F_3 , 25 which segregated in the ratio 15 : 1, and 18 which segregated in the ratio 3 : 1. We have thus 37 : 25 : 18 or 6.94, 4.69, 3.37 in 15, against the expected ratio 7 : 4 : 4, the ratio of the respective numbers of these classes of F_2 individuals, as revealed by their behavior in F_3 generation, being well within the range allowed by the theory.

In the preceding paragraph I have merely described the mode of segregation of various classes of F_2 plants in the F_3 generation. In order to study the behavior of F_3 plants in the F_4 generation, we must first of all contemplate their genetical formulae, which are enumerated below, and compare with those of the F_2 plants from which each of them is derived, respectively. The variegated plants are enclosed in brackets.

	F_2	F_3
Class 1	$GGHH$	$GGHH$
	$GgHH$	$GGHH, GgHH, ggHH$
	$GGHh$	$GGHH, GGHh, GGhh$
	$GGhh$	$GGhh$
	$ggHH$	$ggHH$
Class 2	$GgHh$	$\left\{ \begin{array}{l} GGHH (1), GgHH (2), GGHh (2) \\ GGhh (1), ggHH (1), GgHh (4) \\ ggHh (2), Gghh (2), [gghh] (1) \end{array} \right.$
Class 3	$\left\{ \begin{array}{l} ggHh \\ Gghh \end{array} \right.$	$\left\{ \begin{array}{l} ggHH (1), ggHh (2), [gghh] (1) \\ GGhh (1), Gghh (2), [gghh] (1) \end{array} \right.$
Class 4	$[gghh]$	$[gghh]$

If we look at the formulae of F_3 plants of various classes enumerated above, it will be easily seen that our expectation in F_4 should be as follows:

1. All individuals belonging to class 1, derived from green F_2 plants with no segregation of variegated plants, should again give green plants only;

2. Individuals belonging to class 2 should contain three kinds of green individuals: namely, those breeding true to greenness [$GGHH$ (1), $GgHH$ (2), $GGHh$ (2), $GGhh$ (1), $ggHH$ (1)]; those segregating in the ratio 15 : 1 [$GgHh$ (4)]; and those segregating in the ratio 3 : 1 [$ggHh$ (2), $Gghh$ (2)], the respective numbers of these three kinds of individuals being in the ratio 7 : 4 : 4;

3. Green individuals belonging to class 3 should be of two kinds, namely those which breed true to greenness [$ggHH$ (1) and $GGhh$ (1)], and those which segregate in the ratio 3 : 1 [$ggHh$ (2) and $Gghh$ (2)], the ratio of these two kinds of individuals being 1 : 2.

Let us see now whether or not this expectation is fulfilled.

For this purpose I have cultivated in 1915, 10 F_3 plants of class 1, 129 of class 2 and 68 of class 3, altogether seeds were secured from each of 207 of them by self-fertilization, and sown immediately after

their collection. Unfortunately many of these seeds failed to germinate and no results whatever were obtained in this year, so that the examination of the segregation of the F_3 plants was postponed till 1916. In the latter year, however, many plants grown in 1915 had perished and only 108 plants remained with which to continue the experiment. These plants were:

1. Those of class 1. Only one or two F_3 plants derived from F_2 plants of each of the pedigree Nos. 3, 4, 5, 17, 46, 54, 55, 62, 63, 78,—17 in all (table 4);

2. Those of class 2. One to six F_3 plants derived from F_2 plants of each of the pedigree Nos. 11, 15, 25, 27, 35, 38, 44, 45, 48, 52, 72, 73, 74, 76,—65 in all (table 5 A);

3. Those of class 3. One to four F_3 plants derived from F_2 plants of each of the pedigree Nos. 7, 12, 13, 39, 58, 70, 71,—26 in all (table 5 B).

Plants arising from seeds of the above-mentioned 108 plants, by self-fertilization, were examined in 1916 and results are shown in tables 4, 5 and 6.

Table 4 represents the behavior of F_3 plants of class 1 and it will be seen that 11 of them produced green plants only.⁴

Green individuals belonging to class 2 may be distinguished as of three kinds, as we have expected, and these are shown in table 5 A. Of these three kinds those shown in the first part of this table breed true to greenness. In the second part are progenies aggregating 3428 green and 250 variegated plants, or 14.912 and 1.088 per 16; $\alpha = \pm 0.088$, while $E_M = 0.043$, the segregation in the ratio 15:1 being thus proven. The individuals shown in the third part of table 5 A yielded progenies consisting of 2763 green and 765 variegated plants or 3.133 and 0.867 per 4, i. e., $\alpha = \pm 0.133$, while $E_M = \pm 0.020$. Thus in the last case the deviation from expectation is more than six times the probable error. At the time the families entered in this table were grown, the seedlings were counted in a pretty advanced stage of their development, so that there should have been no such mistakes as were perhaps made in counting the seedlings in table 3, when it was not known that some variegated plants have green cotyledons (see p. 395); besides this deviation is much wider than in that case. This deviation is, as will be seen from the table, due to the insufficiency of the number of variegated plants and this latter fact may be probably explained by the weakness of variegated plants. From my long ex-

⁴ The number of the F_3 progeny of this class was not counted, as noticed on p. 394.

perience in the cultivation of the variegated variety of *Plantago*, I have found that they, like variegated forms of other plant species, are of very weak constitution, this being due of course to their inadequate nutrition. Thus it was natural also to assume that the germination of their seeds is on the whole much poorer than that of normal green plants. To compare the rate of germination of seeds of both races sowings were made⁵ and the number of seeds sown was compared with that of those which had germinated. The results are shown in tables 6 and 7. From these we see that even in the green plants the rate of germination is not very high (66.76 percent, table 6),⁶ but in variegated plants it is much lower (45.41 percent, table 7). The insufficiency of the number of variegated plants above referred to, may in all probability be explained by this difference between the percentage germination of seeds of the two races. In table 7 it may be noted that in variegated plants the rate of germination is quite different in different individual spikes; thus in Nos. 9, 10 and 13 it is much higher than the average

TABLE 4

Pedigree No. of F ₂ plants	Pedigree No. of F ₃ plants	F ₄ generation		
		Number of green	Number of variegated	Totals
3	1	266	0	266
	2	99	0	99
4	1	301	0	301
	2	412	0	412
5	1	213	0	213
	2	227	0	227
17	1	179	0	179
	2	433	0	433
46	1	274	0	274
	2	256	0	256
54	1	296	0	296
	2	210	0	210
55	1	185	0	185
62	1	280	0	280
	2	153	0	153
63	1	273	0	273
78	1	151	0	151
Totals		4208	0	4208

⁵ Seeds were sown generally on the very day of their collection or sometimes on the day immediately following.

⁶ As is well known the seeds of *Plantago* are very minute and consequently very poor in nutritive substances, which will perhaps account for their poor germination.

TABLE 5 A

Pedigree No. of F ₂ plants	Pedigree No. of F ₈ plants	F ₄ generation			
		Number of green	Number of variegated	Totals	Ratio of green to variegated
11	1	136	0	136	
15	4	152	0	152	
	5	160	0	160	
	2	141	0	141	
25	3	435	0	435	
	6	489	0	489	
	1	86	0	86	
	3	96	0	96	
27	5	31	0	31	
	7	201	0	201	
	8	74	0	74	
	9	199	0	199	
38	1	59	0	59	
	2	48	0	48	
44	4	267	0	267	
	5	319	0	319	
	1	399	0	399	
45	3	104	0	104	
	4	409	0	409	
	2	119	0	119	
48	4	50	0	50	
	6	253	0	253	
	2	301	0	301	
	4	346	0	346	
52	7	247	0	247	
	8	200	0	200	
	10	338	0	338	
	1	338	0	338	
72	2	170	0	170	
	3	131	0	131	
74	1	249	0	249	
	4	286	0	286	
Totals		6833	0	6833	
15	3	86	5	91	15.121 : 0.879
	4	111	6	117	15.179 : 0.821
25	5	122	11	133	14.677 : 1.323
	2	100	6	106	15.094 : 0.906
27	4	128	13	141	14.525 : 1.475
	6	303	22	325	14.917 : 1.083
44	3	305	26	331	14.743 : 1.257
45	5	155	15	170	14.588 : 1.412
48	5	176	9	185	15.222 : 0.778

TABLE 5 A (continued)

Pedigree No. of F ₂ plants	Pedigree No. of F ₃ plants	F ₄ generation			
		Number of green	Number of variegated	Totals	Ratio of green to variegated
52	1	162	14	176	14.727 : 1.273
	3	267	20	287	14.885 : 1.115
	6	183	12	195	15.015 : 0.985
	9	249	18	267	14.921 : 1.079
	11	334	24	358	14.927 : 1.073
72	4	195	16	211	14.787 : 1.213
73	1	40	3	43	14.884 : 1.116
74	3	449	28	477	15.061 : 0.939
76	1	63	2	65	15.508 : 0.492
Totals		3428	250	3678	14.912 : 1.088
11	3	264	76	340	3.106 : 0.894
	4	21	8	29	2.897 : 1.103
15	2	239	75	314	3.045 : 0.955
35	2	279	85	364	3.066 : 0.934
44	1	93	27	120	3.100 : 0.900
45	2	193	44	237	3.257 : 0.743
	7	380	99	479	3.173 : 0.827
48	1	122	31	153	3.190 : 0.810
	3	226	69	295	3.064 : 0.936
52	5	166	36	202	3.287 : 0.713
	12	135	25	160	3.375 : 0.625
72	5	146	34	180	3.244 : 0.756
73	2	84	21	105	3.200 : 0.800
74	2	95	26	121	3.140 : 0.860
	5	320	109	429	2.984 : 1.016
Totals		2763	765	3528	3.133 : 0.867

rate in green plants, (table 6), while in Nos. 5, 11, 14, 16, etc., it is very low and in No. 7 exceptionally poor. The insufficiency of the number of variegated plants in the third section of table 5 A may have been due to the fact that it included a large number of spikes containing seeds of variegated plants having poor germinating power. From all these considerations we may well conclude that in the families presented in the third section of table 5 A, the segregation took place in the ratio 3 : 1, though the deviation is somewhat greater than expected by the theory.

As will be seen from table 5 A there are three categories of green individuals of class 2; namely, those breeding true, those segregating

TABLE 5 B

Pedigree No. of F ₂ plants	Pedigree No. of F ₈ plants	F ₄ generation			
		Number of green	Number of variegated	Totals	Ratio of green to variegated
7	4	144	0	144	
	5	58	0	58	
12	5	55	0	55	
39	3	203	0	203	
58	1	283	0	283	
	1	222	0	222	
70	3	128	0	128	
71	4	209	0	209	
	2	60	0	60	
Totals		1362	0	1362	
7	2	114	47	161	2.832 : 1.168
	3	132	47	179	2.950 : 1.050
	6	159	60	219	2.904 : 1.096
12	2	73	28	101	2.891 : 1.109
	3	279	98	377	2.960 : 1.040
	4	186	72	258	2.884 : 1.116
	6	108	34	142	3.042 : 0.958
13	1	224	63	287	3.122 : 0.878
	2	18	10	28	2.571 : 1.429
	3	162	43	205	3.161 : 0.839
	4	102	34	136	3.000 : 1.000
39	1	235	69	304	3.092 : 0.908
	2	188	78	266	2.827 : 1.173
	4	20	6	26	3.077 : 0.923
58	2	41	15	56	2.929 : 1.071
	3	66	24	90	2.933 : 1.067
71	1	152	47	199	3.055 : 0.945
Totals		2259	775	3034	2.978 : 1.022

in 15 : 1, and those segregating in 3 : 1, and these three categories are present in the respective numbers 32 : 18 : 15, or 7.39 : 4.15 : 3.46 in 15, which is very near to the theoretical expectation 7 : 4 : 4.

As to green individuals of class 3 we should have, as already stated on p. 397, two categories; namely, those breeding true and those repeating the segregation in the ratio 3 : 1, the number of individuals of these two categories being 1 : 2. In the first section of table 5 B are given those of the first category, all of which breed true. In the second part of the table we have a total of 2259 green and 775 variegated plants, or 2.978 and 1.022 respectively in 4; $a = \pm 0.022$, while $E_M = \pm 0.021$,

TABLE 6
Green F₂ plants breeding true.

No. of spikes	Number of seeds sown	Number of seeds germinating	Rate of germination in percent
1	396	266	67.17
2	434	99	43.84
3	542	301	55.54
4	562	412	73.31
5	308	213	69.16
6	276	227	82.25
7	308	179	58.12
8	636	433	68.08
9	312	274	87.82
10	338	256	75.74
11	359	296	82.45
12	285	210	73.68
13	315	185	58.73
14	372	280	75.27
15	256	153	64.97
16	351	273	77.78
17	253	151	59.68
Totals	6303	4208	66.76

TABLE 7
Variegated plants.

No. of spikes	Number of seeds sown	Number of seeds germinating	Rate of germination in percent
1	316	149	47.15
2	251	103	41.04
3	168	96	57.14
4	279	120	43.01
5	277	92	33.21
6	110	71	64.54
7	148	14	9.96
8	198	126	63.64
9	90	67	74.44
10	132	103	78.03
11	159	60	37.74
12	202	88	43.56
13	71	64	90.14
14	249	62	24.90
15	305	148	48.52
16	353	137	38.81
Totals	3308	1502	45.41

expectation being thus pretty well fulfilled. Again, examination of table 5 B reveals the fact that there were 9 individuals breeding true (first section) and 17 segregating (second section), or 1.038 : 1.962, which almost perfectly fulfills the expectation above stated concerning the relative numbers of these two categories of individuals belonging to class 3.

Thus all results secured in F_4 progenies are pretty well in accordance with the theoretical expectation.

No further generations than F_4 were studied, but it is quite evident that F_5 , F_6 , etc., would give a repetition of the behavior here described for F_3 and F_4 .

GENOTYPIC NATURE OF THE CONSTANT GREEN PLANTS

We have seen that there are some F_2 individuals which breed constantly green throughout successive generations, for instance Nos. 3, 4, 5, etc. Although all these green plants breed true by self-fertilization they are not all of the same genetical nature; or, in other words, they are *phenotypically*, but not necessarily *genotypically equal*. As shown on p. 397, individuals should be included in this group which have the genotypic formulae $GGHH$, $GgHH$, $GGHh$, $GGhh$ and $ggHH$. To distinguish between these classes of genotypically different green plants it is necessary first to hybridize each of them with a variegated plant and to examine the progeny derived from the hybrids thus made. Then it will be easily seen that the hybrid $GGHH \times gghh$ will give green and variegated offspring in the ratio 15 : 1, $GGhh \times gghh$ and $ggHH \times gghh$ in 3 : 1, while in $GgHH \times gghh$ as well as $GGHh \times gghh$, one-half will segregate in 15 : 1 and the other in 3 : 1.

To test the correctness of these assumptions, a number of constant green F_2 plants were selected at random and hybridized with a variegated plant, a large quantity of seeds being produced. Many of these failed to germinate, but fortunately I secured a number of hybrids sufficiently large for the purpose of the experiment. The constant green F_2 plants belonged to the pedigree Nos. 17, 54, 55, 62, 63, 64 and 78, and in 1915 I obtained from them 73 hybrids, all of which were self-colored green, the variegation being recessive. The self-fertilization of these hybrids in 1916 gave the results shown in table 8.

On examining the results shown in this table, the progenies of Nos. 17.I, 54.IX and 55.II, which are enclosed in brackets, should first be noted. The self-fertilization of these three plants gave not a single variegated offspring. As each of them was supposed to be a hybrid

TABLE 8

Pedigree No. of F ₂ plants	Pedigree No. of F ₂ green × variegated	Progeny of F ₂ green × variegated			
		Number of green	Number of variegated	Totals	Ratio of green to variegated
17	[I]	[55]	[0]	[55]	[1.000 : 0.000]
	II	1084	71	1155	15.016 : 0.984
	III	93	36	129	2.884 : 1.116
54	I	308	98	406	3.034 : 0.966
	II	162	40	202	3.208 : 0.792
	III	387	141	528	2.932 : 1.068
	IV	229	60	289	3.170 : 0.830
	V	258	17	275	15.011 : 0.989
	VI	321	83	404	3.178 : 0.822
	VII	250	83	333	3.001 : 0.999
	VIII	13	6	19	2.737 : 1.263
	[IX]	[144]	[0]	[144]	[1.000 : 0.000]
55	I	221	77	298	2.966 : 1.034
	[II]	[295]	[0]	[295]	[1.000 : 0.000]
	III	262	83	345	3.038 : 0.962
	IV	110	38	148	2.973 : 1.027
	V	124	42	166	2.988 : 1.012
	VI	119	52	171	2.784 : 1.216
	VII	94	39	133	2.827 : 1.173
	VIII	106	35	141	3.007 : 0.993
	IX	32	12	44	2.909 : 1.091
	X	68	21	89	3.056 : 0.944
	XI	24	9	33	2.909 : 1.091
	XII	9	5	14	2.571 : 1.429
	XIII	26	18	44	2.364 : 1.636
62	I	242	19	261	14.835 : 1.165
	II	456	27	483	15.106 : 0.894
	III	244	76	320	3.050 : 0.950
	IV	175	62	237	2.954 : 1.046
	V	471	44	515	14.633 : 1.367
	VI	194	61	255	3.043 : 0.957
	VII	117	34	151	3.099 : 0.901
	VIII	87	34	121	2.876 : 1.124
	IX	235	43	278	3.381 : 0.619
	X	215	13	228	15.088 : 0.912
	XI	249	27	276	14.435 : 1.565
	XII	229	72	301	3.043 : 0.957
	XIII	163	14	177	14.734 : 1.266
	XIV	277	86	363	3.052 : 0.948
	XV	64	3	67	15.284 : 0.716
	XVI	186	14	200	14.880 : 1.120
	XVII	187	13	200	14.960 : 1.040
	XVIII	552	36 ^r	588	15.020 : 0.980
	XIX	43	13	56	3.071 : 0.929

^r Including two perfectly white seedlings which died soon after their germination.

TABLE 8 (continued)

Pedigree No. of F ₂ plants	Pedigree No. of F ₂ green × variegated	Progeny of F ₂ green × variegated			
		Number of green	Number of variegated	Totals	Ratio of green to variegated
62	XX	161	25	186	3.462:0.538
	XXI	183	61	244	3.000:1.000
63	I	75	5	80	15.000:1.000
	II	302	21	323	14.960:1.040
	III	60	9	69	3.478:0.522
	IV	128	9	137	14.949:1.051
	V	136	13	149	14.604:1.396
	VI	49	3	52	15.077:0.923
	VII	42	2	44	15.273:0.727
	VIII	138	13	151	14.623:1.377
	IX	164	13	177	14.825:1.175
	X	108	12	120	14.400:1.600
64	I	361	27	388	14.887:1.113
	II	259	15	274	15.124:0.876
	III	263	24	287	14.662:1.338
	IV	175	9	184	15.217:0.783
	V	346	32	378	14.646:1.354
	VI	147	12	159	14.792:1.208
	VII	193	7	200	15.440:0.560
	VIII	199	26	225	14.151:1.849
	IX	49	4	53	14.792:1.208
	X	131	9	140	14.971:1.029
78	I	154	60	214	2.879:1.121
	II	108	49	157	2.752:1.248
	III	236	63	299	3.157:0.843
	IV	209	59	268	3.119:0.881
	V	322	120	442	2.914:1.086
	VI	54	27	81	2.667:1.333
	VII	69	17	86	3.209:0.791
	Totals	7392	554	7946	14.884:1.116
		6115	1949	8064	3.033:0.967

green × variegated, self-fertilization should have resulted in progenies consisting of both green and variegated plants. The fact that no variegated plants were produced must be accounted for. Two alternative explanations suggest themselves. On the one hand these cultures might be assumed to represent extreme cases of elimination of variegated plants through failure to germinate, owing to their constitutional weakness. It is indeed true, as already shown, that variegated plants

are generally weaker in their bodily constitution than green ones, and also that the percentage germination of seeds is lower in the former than in the latter. In spite of these facts it is very improbable that no single variegated plant should have appeared if segregation really took place, because in 55.II, for instance, where 295 green plants appeared, more than 18 variegated plants should have been expected on the basis of the lowest available ratio, 15 : 1. Besides the progeny shown in the table, I have secured another consisting of more than 700 plants by saving seeds from two spikes of the same pedigree number, and yet no single variegated plant was secured. From these results I came to the conclusion that no segregation had here taken place and the first of the two alternative explanations was rejected. The second one, which is much more probable, and which I have adopted to account for the facts observed, is that these three families were from constant green plants which had slipped into the cultures through an error in technique, in spite of our utmost care to avoid such mistakes. This interpretation will not be considered at all improbable in view of the large extent of these *Plantago* cultures. The numbers of green plants in the progenies of these three plants are not counted in the totals, though they are included in the table for the sake of completeness, and are distinguished by enclosure in brackets.

A further point to be noted in table 8 concerns pedigree Nos. 62.XX and 63.III.

In the former the deviation (α) of the number of segregates for 4 or 16 is much larger than would be expected theoretically. According as this family is assumed to exhibit the 3 : 1 or 15 : 1 ratio, $\alpha = 0.462$ and $E_M = \pm 0.086$, or $\alpha = 1.151$ and $E_M = 0.192$, respectively, α being thus larger than $3E_M$ in either case. A definite determination as to whether this family exhibited the 3 : 1 or 15 : 1 segregation would be possible only by raising the progeny of later generations, but as all plants derived from this number perished long ago, the determination of this question is now impossible. The classification of this family, provisional as it was, was made in the following way: The quotient,

$$\frac{\text{deviation}}{\text{probable error of the mean}} = \frac{\alpha}{E_M}, \text{ when referred to the ratios } 3 : 1$$

or 15 : 1, respectively, gives a measure of the relative closeness of fit of the observed results to either of these theoretical ratios. The family was classed under that ratio which gave the smaller quotient. This

quotient is $\frac{0.462}{0.086} = 5.372$ or $\frac{1.151}{0.192} = 5.995$, according as the family

in question is considered to belong to the one or the other of these two classes, and as the former quotient is the smaller, this culture was put

in the class 3 : 1. In No. 63.III the quotient $\frac{a}{E_M}$ is $\frac{0.478}{0.140} = 3.414$

or $\frac{1.087}{0.314} = 3.462$, respectively, and this family was put also in the class

3 : 1, in which the quotient is a trifle smaller.

Having disposed of these two doubtful families, let us now examine the general results as shown in table 8. If we sum up all the green plants derived from individuals whose progenies show segregation in the ratio 15 : 1, on the one hand, and all of the variegated plants of the same families, on the other hand, we have 7392 green and 554 variegated plants, or 14.884 to 1.116, respectively; thus $a = \pm 0.116$, while $E_M = \pm 0.029$. In the case of individuals considered to have segregated in 3 : 1 the corresponding calculation gives 6115 green and 1949 variegated plants, or 3.033 and 0.967, respectively; $a = \pm 0.033$, $E_M = \pm 0.013$. Thus although the deviations from expectation are not very small, yet they are not so large as to lie beyond the limits prescribed by theory.

Furthermore, from the examination of the table we see that there are three categories of F_2 individuals, namely,

1. Those which, being crossed by a variegated plant, give hybrids all of which segregate in 15 : 1. No. 64 belongs to this class.

2. Those of which all hybrids made by the same process, segregate in 3 : 1, to which class Nos. 55 and 78 belong.

3. Those of which hybrids made in similar way segregate partly in 15 : 1 and partly in 3 : 1, to which belong Nos. 17, 54, 62, and 63.

We may therefore represent No. 64 by $GGHH$, Nos. 55 and 78 by $GgHh$ or $ggHH$, and Nos. 17, 54, 62, and 63 by $GGHh$ or $GgHH$. Besides, as we have already seen on page 394, the number of constant green plants in the F_2 generation should be 7 in every 15, and of these 7, according to theoretical expectation, we should have the three classes just mentioned, in the ratio 1 : 2 : 4.⁸

⁸ $GGHH$ 1, $GgHh$ 1, $ggHH$ 1, $GgHH$ 2, $GGHh$ 2.

In table 8 we see that plants of these three classes, as revealed by experiment, occurred in the respective numbers of 1 : 2 : 4, which by chance exactly correspond to the theory.

Furthermore, $GGHh \times gghh$ and $GgHH \times gghh$ should each segregate either in 3 : 1 or 15 : 1, and individuals belonging to these two categories of segregation are expected to occur in *equal* numbers. Now if we examine table 8, we have in No. 17 only one individual from each class; this number is too small, however, for judging whether our expectation is fulfilled; in No. 62 we have 11 families showing 3 : 1 segregation and 10 which show a 15 : 1 ratio, a result which is as near as possible to expectation; while in Nos. 54 and 63 the numbers of plants exhibiting these two classes of segregation are very unequal. If the individuals of these four pedigrees are combined, the expectation is almost perfectly fulfilled, as shown in table 9.

TABLE 9

Pedigree No.	3 : 1	15 : 1
17	1	1
54	7	1
62	11	10
63	1	9
Totals	20	21

HAVE WE A CASE OF POLYMERY IN THE GREEN RACE OF PLANTAGO?

The production of a certain given character by the action of two or more independent factors or genes, each of which when separated from the other, is able to produce the same character, is a well known phenomenon, since the appearance of the important researches of NILSSON-EHLE (1909), and is called by different names by different authors. "*Polymery*" was first proposed by LANG (1911, p. 113) to designate this phenomenon. PLATE (1913, p. 155) introduced the word "*homomery*" instead of polymery. JOHANSEN (1913, pp. 560-561) has distinguished two classes of polymery,—cumulative and non-cumulative. In the former case the action produced by two or more genes acting simultaneously is quantitatively larger than when but one is present, or in other words, the action of several genes accumulates; while in the latter class one single gene is able to perform a function both qualitatively and quantitatively equal to that produced by the conjoint action of several genes. JOHANSEN reserves the name "*homomery*" for this latter class of polymery.

That several genes participate in the production of a given character is a very common phenomenon, but this does not necessarily represent a case of polymery, because in polymery two or more genes, each performs nearly the same function, while genes of very different functions may act together for the development of one character. For instance, according to BAUR (1910, p. 89) the green leaf color of *Antirrhinum* is due to three independent factors Z , Y and N , so that we have the formula $ZZYYNN$ for the full green color. In this case three genes appear to act together to produce one character, but their respective functions were found to differ from each other, so that we have here no case of polymery. SHULL (1914 b) has shown a similar constitution with respect to chlorophyll factors in *Lychnis dioica* L. but in this case the factors Y and N seem to have more nearly like functions, the presence of either resulting in the production of chlorophyll, though not in equal amounts. Only in the presence of both Y and N are the plants dark green as in the wild species. To avoid the confusion between such a case and true polymery SHULL (1914 a, p. 120) has proposed the expressions "plural determiners" and "duplicate determiners." By "duplicate determiners" he means, "those which, when separated from each other, produce characters so like that they cannot be distinguished from one another", while by "plural determiners" he designates "those which independently produce a given character, or which modify it in any way whatever, which does not destroy its identity". Thus the duplicate determiners, which are a special case of plural determiners, correspond to polymery in the sense of LANG, while the plural determiners, not only include polymery, but also such cases as exemplified above in *Antirrhinum*, where several genes of different functions act conjointly for the production of one given character.

The question to be decided is whether or not the green race of *Plantago* here described represents a case of polymery. It has been demonstrated by the experiments here described, that the original green parent has the genetical formula $GGHH$ in respect to its green color. When it is crossed with a variegated plant we have in F_2 as well as in later generations various zygotes containing either one or both genes G and H , as for instance $GGHH$, $GGhh$, $GgHh$, etc., yet all these are self-colored green like the original green parent. It is evident therefore that we have here a clear case of polymery.

We may further ask, whether or not any difference can be detected in the intensity of the green color according to the number of genes contained in each zygote, or in other words, is polymery in this case

cumulative or non-cumulative in the sense of JOHANNSEN? Had we here a case of cumulative polymery we should find in F_2 and the succeeding generations plants of several gradations in respect to the intensities of their green color, because then we would have plants containing two kinds of genes in various combinations. During the earlier generations I paid no special attention to this question and there might have been possibly such slight differences which escaped my eyes. Observations and experiments were specially made in 1916 to detect such differences, if any existed. In that year I had in cultivation, a large number of F_2 plants of very different genetical constitutions; thus we had those represented by $GgHh$ (segregating in 15 : 1 in F_3), others represented by $Gghh$ or $ggHh$ (segregating in 3 : 1 in F_3) and still others breeding true to greenness, which according to the results shown in table 8, are to be represented variously by $GGhh$ (or $ggHH$), $GGHh$ (or $GgHH$) and $GGHH$, thus we see that some zygotes contain only one kind of gene, others contain both, yet by careful comparison of these zygotes without the use of special colorimetric methods, I could not recognize any appreciable difference in the intensities of their green color. The following colorimetric experiment was then undertaken: From the leaves of nearly the same age on F_2 plants, Nos. 3, 4, 12, 17, 25, 46, 55, 62, 63, 78 (all constant green except 12 and 25), pieces of equal size (two from each leaf) were cut off by means of a cork-borer, according to the method adopted by CORRENS (1903, p. 140), and immersed separately in equal quantities of 90 percent alcohol in test-tubes of the same size. After a few days, alcoholic solutions of chlorophyll thus made were placed side by side to compare the intensities of their green color. Of the 10 individuals above enumerated, from each of which a chlorophyll solution was made, the genetical formulae of five were known, namely, Nos. 12 ($Gghh$ or $ggHh$), 17 ($GGHh$ or $GgHH$), 25 ($GgHh$), 55 and 78 ($GGhh$ or $ggHH$). As to the remaining five zygotes, their exact genetical constitution is not known, but it might be expected that among these constant green plants were individuals which could be represented by $GGHH$, $GGHh$, $GgHH$, $GGhh$, $ggHH$. In spite of such diversities in their genetical constitution I was unable to detect any appreciable difference at all between the intensities of the green color of the chlorophyll solutions which were made from leaves of these several plants, by means of the method just described. A comparison by the colorimetric method was made between the green parent and the F_1 plants produced by crossing it with a variegated plant. The plants used in my original cross having perished long before the time

when this experiment was undertaken, I simply transplanted into the garden a wild green plant growing in the place where the green parent of my original cross was collected, and hybridized it by a variegated plant. This new green plant had the same formula as the original green parent, i. e., *GGHH*, as revealed by the mode of segregation exhibited in F_2 . Seeds from five spikes from as many different F_1 plants were sown and seedlings arising from them were counted separately, giving in F_2 the results shown in table 10. It is evident therefore that the F_1

TABLE 10

No. of spikes	No. of green	No. of variegated	Totals
1	50	4	54
2	150	7	157
3	26	1	27
4	63	6	69
5	30	2	32
Totals	319	20	339
or	15.056	0.944	16

$$a = \pm 0.056, E_M = \pm 0.146$$

plant has the formula *GgHh*. I made chlorophyll solutions from both plants in the way above indicated, compared them with each other as well as with each of the former series of chlorophyll solutions, but in this case also I was unable to detect any appreciable difference between the color intensities of these solutions.⁹

From the results of all these observations, either directly by eye without special aids, or by colorimetric methods, we have concluded that neither by the conjoint action of two or more genes of the same category nor by that of two or more genes of the different categories does any appreciable intensification of the color take place; thus only one gene is able to give rise to a reaction exactly equal to that produced by several genes acting together. In other words, we see here the complete dominance of genes, demonstrating that this is homomery or non-cumulative polymery, in the sense of JOHANNSEN.¹⁰

⁹ Chlorophyll solutions were also made from leaves of variegated plants and compared with those of green plants in the same manner as above indicated and it was quite evident that their green color is much less intense.

¹⁰ It is not absolutely certain of course that had I employed much finer methods of colorimetric determination than were actually used, some differences of intensity of the green color might have been detected, but I may perhaps be allowed to say that if such differences exist they must be slight in the extreme and of no special importance.

COMPARISON WITH OTHER RACES

The hereditary behavior of certain variegated plants has been studied by some other authors. Variegated plants which follow Mendel's law when crossed with green plants, have always been found hitherto to segregate in F_2 in the ratio of approximately three green to one variegated (CORRENS 1909, BAUR 1910). Only in maize has EMERSON (1912, p. 94) found in some few cases ratios varying from 9 : 1 to 26 : 1 in F_2 , and he thinks it possible that there are two factors involved, such that only in the absence of both is the plant variegated, but no further observations on this case have been reported. The variegated race of *Plantago* described in this paper is thus a new case, in so far as the presence of two duplicate factors has been duly proven, only in the absence of both of which is the plant variegated.

The fact that there are two or more factors for chlorophyll production has been discovered in some other cases, not by means of variegated plants as in our case, but by means of nearly pure white plants ("chloralbinos", SHULL 1914 b), or to borrow the expression of NILSSON-EHLE (1911, p. 18), by using the chloralbino instead of a variegated plant as an "analyzer." Thus, for instance, according to MILES (1915), in some varieties of maize the normal green plant has the formula *AABB*; plants represented by *aabb* and *AAbb* are pure white, while those represented by *aaBB* are yellowish-white, so that we have in this case two factors for green color, but since *AAbb* is different from *aaBB* we have here no polymery. In *Senecio vulgaris*, however, according to the investigations of TROW (1916) both *S. praecox* and *S. lanuginosus* are fully green, yet *praecox* \times *lanuginosus* segregates in F_2 into 15 green to 1 white. It appears therefore that *praecox* and *lanuginosus*, both fully green, may be represented respectively by *AAbb* and *aaBB* and that among 15 green plants appearing in F_2 , one fully green plant, represented by *AABB*, is found. Thus we have in the latter plant a case of polymery very similar to our green race of *Plantago*, though naturally it is unknown whether or not the factors *G* and *H* in *Plantago* are identical with *A* and *B* in *Senecio*.

THE PRODUCTION OF GREEN PLANTS FROM VARIEGATED

At the beginning of my culture experiments variegated plants seemed to breed perfectly true to type, but later it was discovered that a few fully green plants are produced from them even by self-fertilization. This fact is no new observation, however, because CORRENS (1909), BAUR (1910), and somewhat later, MILES (1915), have observed the

same phenomenon in *Mirabilis*, *Aquilegia* and maize, respectively. According to the first of these three authors green plants thus arisen, either breed true or segregate into green and variegated in various proportions. In *Plantago* I have secured only a very few green plants of such origin; all of these have segregated into green and variegated, and I have found that the ratio of these two segregates has not been 15 : 1, as might be expected from the observations described above, but always approximately 3 : 1, as indicated in table II.

TABLE II

No. of spikes	No. of green	No. of variegated	Totals
1	110	37	247
2	39	15	54
3	60	21	81
Totals	209 2.965	73 1.035	282 4

$$\alpha = \pm 0.035, E_M = \pm 0.069$$

No true-breeding green plants have yet been secured from variegated parents, but this may be due to the smallness of the number of green plants of such origin whose progeny I could examine. It seems not improbable that the cultivation of a much larger number of plants would yield such true-breeding plants as well as others which would segregate in the 15 : 1 ratio.

In the Mendelian hybrids thus far studied, green is always dominant over variegated, so that the production of green plants from variegated parents is a very remarkable phenomenon, whereby recessives give rise to dominants. In this connection it may be remarked that I could observe a very similar fact in another race of *Plantago*, concerning a character wholly different from the color.¹¹ From all my observations in respect to such phenomena I have been led to the view that in such cases we are dealing in all probability with the same category of phenomena, as that which is called "vegetative hybridization" (or "autohybridization") or a "recurring somatic variation", by CORRENS (1910) and EMERSON (1914),¹² respectively. My breeding experiments concerning this subject are under way and I hope to be able to publish the results of my investigations in a future paper.

¹¹ The breeding experiment of this race is now in its third year.

¹² EMERSON (1917) has recently changed the expression "somatic variation" to "sporophytic variation." [Note added in correcting the proof.]

SUMMARY

1. A variegated race of *Plantago major asiatica* was found to breed true to its type generally by self-fertilization, though sometimes it produced a few self-colored green plants by the same process.

2. The F_1 hybrids made between the variegated and the ordinary self-colored green plant, whether green \times variegated or variegated \times green, are in either case self-colored green, the latter condition being perfectly dominant over the variegation.

3. The self-colored green plant used as one of the parents in this experiment, was found to contain two factors, called *G* and *H*, respectively, such that the plant is variegated only in the absence of both of them. This fact has been fully demonstrated by the examination of the F_2 , F_3 and F_4 progenies derived from the green \times variegated F_1 hybrid.

4. Each of the two factors above mentioned, even when separated from each other, is able to produce the green color of exactly the same intensity as when both are present together. This is therefore a case of so-called *non-cumulative polymery* or *homomery* in the sense of JOHANNSEN, or the *duplication of factors* in the sense of SHULL.

5. The green F_2 plants which breed true to greenness in successive generations (constant green plants) are not always of the same genetical constitution and their respective genotypic nature has been revealed by hybridizing them with the variegated plants and examining the progenies derived from these hybrids, the F_1 hybrids from such crosses being necessarily self-colored green.

6. Each of the few green plants produced by self-fertilization of variegated plants (cf. 1 of this summary) was found to exhibit segregation in approximately the ratio 3 green to 1 variegated. Breeding experiments concerning this question are under way.

In conclusion, I may add that on account of their extreme minuteness the castration of flowers in *Plantago* is a very delicate operation which requires much patience as well as skill. I take much pleasure in thanking here two gentlemen, Mr. S. NOHARA and Mr. M. ANDÔ, for their kindness in executing this difficult task for me. I wish also to thank Dr. G. H. SHULL, editor of this journal, for revising this paper, as well as for his kindnesses in various other matters.

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STUDIES ON THE PHYSIOLOGY OF REPRODUCTION IN
THE DOMESTIC FOWL. XVII. THE INFLUENCE OF
AGE UPON REPRODUCTIVE ABILITY, WITH
A DESCRIPTION OF A NEW REPRO-
DUCTIVE INDEX¹

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THE PROBLEM

There is a widespread opinion among poultry breeders, which has found its way into the body of poultry husbandry teaching, that it is desirable to use birds two years or more of age for breeding purposes rather than pullets and cockerels one year of age at the time they are bred. Various reasons have been alleged for this view, such as that the progeny from older birds is superior in vigor, or that a more numerous progeny is had per mating, etc. There has never been presented, however, so far as I am aware, any definite quantitative evidence in adequate amount from which one could derive a just conclusion about the influence of age upon the breeding ability of the domestic fowl.

The matter is one of considerable theoretical interest as well as practical importance. With the modern intensive study of genetics the relation of all matters having to do with the physiology of breeding to the age of the animals bred takes on increased theoretical importance. On the practical side it is highly desirable that the breeder should know whether he is actually or potentially reducing the efficiency of his breeding operations if he uses pullets and cockerels as breeders.

It is the purpose of this paper to present some exact numerical evidence regarding the influence of age upon reproductive capacity in fowls of the Barred Plymouth Rock breed. The data on which the paper is based represent the writer's experience at the MAINE AGRICULTURAL EXPERIMENT STATION with this breed for a period of nine consecutive years, during which time exact records have been kept of all the chief factors involved in the reproduction. The number of separate individual

¹ Papers from the Biological Laboratory of the MAINE AGRICULTURAL EXPERIMENT STATION, No. 110.

matings involved is large and it is believed that the results probably represent with substantial accuracy the conditions which will be found to hold generally for this breed.

In attempting the solution of the problem of the influence of age upon reproductive capacity the first essential is an adequate measure of this character. If one considers carefully the question of the measurement of total reproductive capacity in poultry it is at once evident that there are several different factors involved. First and most fundamental is obviously fecundity.² The size of the family which any given mating leaves will evidently in the first instance be determined by the number of eggs which the hen taking part in the mating lays during the breeding period. If she produces only a few eggs, of necessity there can be but few offspring. If she lays many eggs, there may be many or few offspring, the results then being determined by other factors.

The second factor involved in reproductive capacity will be the fertilization of the eggs. If for any reason the male bird in the mating fails to fertilize the eggs, or if the chemical conditions in the oviduct of the female are such as to make it impossible for fertilization to take place, then the number of progeny will be small even though many eggs are laid. The percentage of infertile eggs to the total number of eggs laid is obviously an important factor in the total reproductive capacity of the fowl.

The third important factor is prenatal mortality. A hen may lay many eggs and these may show a high percentage of fertility, but if the embryos are so weak and lacking in vitality that they die before the end of incubation the actual progeny left by the pair of birds in the mating will be by so much reduced. It has been shown by PEARL and

² It is desirable to repeat here the working definition of the terms fecundity and fertility which the writer proposed some years ago, and which have been used throughout the work in this laboratory on problems relating to reproduction in the domestic fowl. PEARL and SURFACE (1909 a) defined these terms as follows: "We would suggest that the term 'fecundity' be used only to designate the innate potential reproductive capacity of the individual organism, as denoted by its ability to form and separate from the body mature germ cells. Fecundity in the female will depend upon the production of ova and in the male upon the production of spermatozoa. In mammals it will obviously be very difficult, if not impossible, to get reliable quantitative data regarding pure fecundity. On the other hand we would suggest that the term 'fertility' be used to designate the total actual reproductive capacity of pairs of organisms, male and female, as expressed by their ability when mated together to produce (i. e., bring to birth) individual offspring. Fertility, according to this view, depends upon and includes fecundity, but also a great many other factors in addition. Clearly it is fertility rather than fecundity which is measured in statistics of birth of mammals."

SURFACE (1909 b) that these two factors, percentage of infertile eggs and percentage of prenatal mortality, are rather highly variable, and to a considerable extent independently of each other. That is, high prenatal mortality may be associated with either high or low fertility of eggs.

The next important factor in the actual reproductive capacity of a bird is the early postnatal mortality. From a broad biological viewpoint the effectiveness of the reproductive processes is measured by the preservation of the species. Any pairing of individuals must leave behind itself sufficient progeny to ensure that some come to maturity and in turn form a new generation. Any of the progeny individuals that die before reaching sexual maturity obviously represent by so much a defective element in the reproductive process. It is a fact well known to poultry breeders that the major portion of chick mortality takes place within the first three weeks after hatching. Under exceptional circumstances, as of epidemics of some contagious disease, there may be a heavy mortality after the birds have attained three weeks of age. The deaths due to innate weakness and lack of constitutional vigor, however, in the main occur, as experience shows, within the first three weeks after hatching. A very large percentage of the chicks alive at three weeks of age may be expected, barring accidents, to live to sexual maturity.

Any quantitative measure of reproductive capacity in the domestic fowl must take into account all of these factors which have been named. They are all variable in rather high degree, and while there is a sensible correlation between some of them in their variation, these correlations are in general low. To put the matter in the other way, these various factors on which reproductive capacity in the domestic fowl primarily depends are, to a considerable degree, independently variable.

Some years ago a poultry breeding index, or, as it was then called a "selection index," was proposed by PEARL and SURFACE (1909 c). The index then proposed was described as follows:

$$I_1 = \frac{5(a+b)}{c+d+1}$$

The following scheme shows the meaning of the letters in the formula:

I_1 = general or fundamental poultry selection index for an individual bird.

a = percentage of this bird's eggs which hatched.

b = percentage of eggs actually laid by this bird to the total number it was possible for her to lay between February 1 and

June 1 (i. e., the breeding season) of the year for which the index is calculated.

c = percentage of this bird's eggs which were infertile.

d = percentage of chicks hatched from this bird's eggs which died within three weeks from the date of hatching.

Practical experience in the use of this index has shown that it has certain defects and fails on that account to meet fully the needs of a satisfactory measure of the total reproductive performance of a mating. A good deal of study has been devoted to the matter of determining a thoroughly satisfactory measure. In the first place, it early became clear that it was a mistake to consider the matter primarily with reference to the female partner in the mating alone. Reproductive capacity or performance in sexually reproducing organisms is obviously a property or characteristic of *matings*; not of individuals. In the second place, it became evident that the more or less independent character of the variation in the several variables involved made the very crude scheme of combination adopted in the original index altogether inadequate. A great deal of time was spent in trying to devise a more complicated and at the same time more adequate scheme of combination of the several variables. While some success was attained, the results were always far from what could be desired.

A NEW REPRODUCTIVE INDEX FOR POULTRY

After much work on the subject it was finally decided to approach the whole problem of the measurement of the total reproductive capacity from a new point of view. This led to the adoption of a new reproductive index for poultry which may be described in the following way:

$$RI = \frac{\text{Number of chickens alive at the end of the 3rd week after hatching} \times 100}{\text{Total number of days from the day when this mating began to the day when the last egg from this mating began its incubation}}$$

The reasoning on which this index is based is as follows: Maximum reproductive capacity, as represented by 100 percent, would be attained if, during the period of the mating, the hens laid one egg every day (maximum fecundity), and if further every one of such eggs was fertile, and if each embryo hatched, and the hatched chick lived to be three weeks of age. There would then be one living chick three weeks of age for each day during which the mating existed. If the hen does *not* lay every day during the mating season this will cause some reduction in the reproductive performance as measured by the index. Similarly a reduction in any of the other factors involved, prenatal or postnatal mortality, will have the same sort of result. The final percentage value which one

obtains by calculating the index will be a true measure of the reproductive capacity of that mating, including within its view *all* of the primary factors of reproduction in poultry.

This proposed index is obviously much simpler to calculate than the old one, and its very simplicity, directness, and obviously logical character commend it at once as the measure for which we are seeking. Actual experience with the index in dealing with data from our matings over a series of years shows that it is an extremely satisfactory and reliable measure of total reproductive performance. It gives a unique numerical expression of just the thing one wants to know, namely the degree to which a mating or pairing of individuals effectively perpetuated itself.

THE INFLUENCE OF AGE UPON REPRODUCTIVE PERFORMANCE IN THE FOWL

We may now turn to a consideration of the problem with which this paper has primarily to do, using the reproductive index as the instrument of research. During the past year my assistant, Mr. JOHN RICE MINER, has calculated the value of this index for all matings which have been made at the MAINE AGRICULTURAL EXPERIMENT STATION poultry plant during the last nine years. In the present paper we shall deal only with the Barred Plymouth Rock matings. Table I shows the

TABLE I

Frequency distribution of reproductive index for Barred Plymouth Rock matings.

Reproductive index	Frequency	Reproductive index	Frequency
- 1.4	195	31.5-33.4	20
1.5- 3.4	68	33.5-35.4	11
3.5- 5.4	88	35.5-37.4	11
5.5- 7.4	82	37.5-39.4	9
7.5- 9.4	83	39.5-41.4	4
9.5-11.4	69	41.5-43.4	4
11.5-13.4	75	43.5-45.4	4
13.5-15.4	83	45.5-47.4	1
15.5-17.4	64	47.5-49.4	1
17.5-19.4	52	49.5-51.4	0
19.5-21.4	47	51.5-53.4	0
21.5-23.4	34	53.5-55.4	0
23.5-25.4	35	55.5-57.4	0
25.5-27.4	33	57.5-59.4	1
27.5-29.4	23	59.5-61.4	2
29.5-31.4	15	Total	1114

Mean

12.496 \pm 0.212

Standard deviation

10.495 \pm 0.150

Coefficient of variation

83.988 \pm 1.864

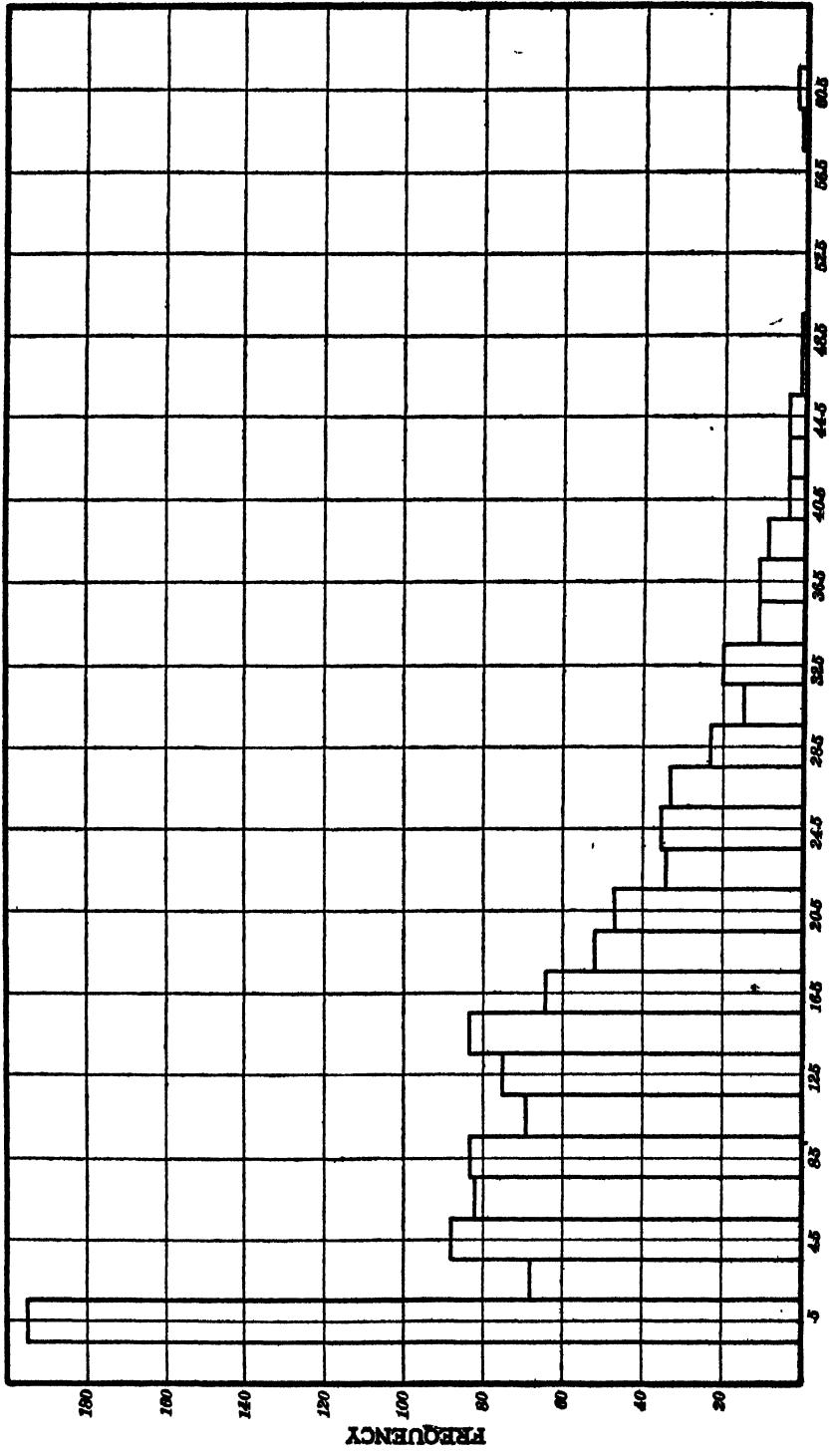


FIGURE 1.—Histogram showing variation in reproductive index.

TABLE 2
Showing the distribution of the reproductive index for each age of sire and dam.

Reproductive Index	Age of											
	Sire=1 Dam=1	Sire=1 Dam=2	Sire=1 Dam=3	Sire=1 Dam=4	Sire=1 Dam=5	Sire=2 Dam=1	Sire=2 Dam=2	Sire=2 Dam=3	Sire=3 Dam=1	Sire=3 Dam=2	Sire=3 Dam=3	Sire=4 Dam=2
—1.4	136	23	1	—	—	12	13	1	6	3	—	—
1.5—3.4	44	10	1	1	—	1	6	1	4	0	—	—
3.5—5.4	57	19	0	—	1	3	6	1	1	0	—	—
5.5—7.4	61	10	0	—	—	3	5	—	2	1	—	—
7.5—9.4	63	11	0	—	—	3	4	—	2	0	—	—
9.5—11.4	46	17	0	—	—	2	1	—	2	1	—	—
11.5—13.4	49	8	2	—	—	4	9	—	2	0	1	—
13.5—15.4	51	13	0	—	—	2	12	—	3	2	—	—
15.5—17.4	51	4	0	—	—	2	7	—	0	0	—	—
17.5—19.4	38	8	1	—	—	3	1	—	1	0	—	—
19.5—21.4	32	6	0	—	—	1	7	—	1	0	—	—
21.5—23.4	21	7	0	—	—	0	4	—	2	0	—	—
23.5—25.4	32	2	0	—	—	0	1	—	0	0	—	—
25.5—27.4	27	4	1	—	—	0	1	—	0	0	—	—
27.5—29.4	21	1	0	—	—	0	1	—	0	0	—	—
29.5—31.4	14	0	0	—	—	0	0	—	0	0	—	—
31.5—33.4	15	2	1	—	—	0	0	—	0	0	—	—
33.5—35.4	10	0	1	—	—	1	0	—	1	1	—	—
35.5—37.4	8	3	—	—	—	—	0	—	—	—	—	—
37.5—39.4	5	3	—	—	—	—	1	—	—	—	—	—
39.5—41.4	4	0	—	—	—	—	—	—	—	—	—	—
41.5—43.4	3	1	—	—	—	—	—	—	—	—	—	—
43.5—45.4	3	1	—	—	—	—	—	—	—	—	—	—
45.5—47.4	—	—	—	—	—	—	—	—	—	—	—	—
47.5—49.4	1	—	—	—	—	—	—	—	—	—	—	—
49.5—51.4	0	—	—	—	—	—	—	—	—	—	—	—
51.5—53.4	0	—	—	—	—	—	—	—	—	—	—	—
53.5—55.4	0	—	—	—	—	—	—	—	—	—	—	—
55.5—57.4	0	—	—	—	—	—	—	—	—	—	—	—
57.5—59.4	1	—	—	—	—	—	—	—	—	—	—	—
59.5—61.4	2	—	—	—	—	—	—	—	—	—	—	—
Totals	796	153	7	1	1	37	79	3	27	8	1	1

value of the reproductive index for 1114 matings of pure-bred Barred Plymouth Rocks, all ages being included in this distribution which is shown graphically in figure 1. A wide range of environmental conditions is represented in the statistics. Some of the years contributing data were extremely good years for hatching and rearing, while others were just as extremely bad. On the whole the statistics are so extensive and the time covered so long that the end result probably is about the average representation of the breed.

From the table and diagram we note at once the following points:

1. There is an unexpectedly large amount of variation in this characteristic. That is, the values obtained from particular matings range all the way from 0 to over 60 percent.

2. Leaving out of account for a moment the first class (values of the index from 0 to 1.5) we see a rather flat-topped distribution over to a value of about 18 percent for the index. Beginning at that point and continuing to the end of the distribution there is a steady falling off in the frequency with high indices.

3. The high value of the first class, including reproductive indices from 0 to 2, arises from the considerable number of wholly sterile matings which give a value for the reproductive index of 0.

In table 2 the data are so arranged as to show the relation of reproductive capacity to age. Separate distributions are given for each age grouping of sire and dam.

The variation constants, with their probable errors, deduced from table 2 are shown in table 3. SHEPPARD'S correction of the second moment was not used, the conditions which warrant its use not being even approximately realized in the distributions.

TABLE 3

Showing the variation constants for reproductive index in Barred Plymouth Rocks.

Age of sire and dam	Mean	Standard deviation	Coefficient of variation
Sire=1, Dam=1	13.083±0.260	10.867±0.184	83.066± 2.166
Sire=1, Dam=2	11.781±0.546	10.016±0.386	85.018± 5.127
Sire=1, Dam=3	15.071±2.775	10.887±1.963	72.237±18.615
Sire=1, Dam=4	2	0	0
Sire=1, Dam=5	4	0	0
Sire=2, Dam=1	8.392±0.866	7.808±0.612	93.039±12.057
Sire=2, Dam=2	11.361±0.623	8.204±0.440	72.216± 5.539
Sire=2, Dam=3	2.500±0.636	1.633±0.450	65.320±24.486
Sire=3, Dam=1	9.389±1.086	8.368±0.768	89.127±13.163
Sire=3, Dam=2	10.000±2.429	10.186±1.718	101.858±30.118
Sire=3, Dam=3	13	0	0
Sire=4, Dam=2	30	0	0

From this table we note:

1. In round figures the reproductive index, in the case of the strain of Barred Rocks here dealt with, and under the general conditions of environment and management at the MAINE STATION poultry plant (PEARL 1916), has an average or mean value of 12.5. It is at present impossible to make any comparisons of these reproductive index figures for the reason that these constants have not been calculated for other conditions. From his own unpublished data, however, the writer is very sure that there will be found large reproductive index differences between different breeds. It is also highly probable that this constant will be found to take different values as climatic and other general environmental factors change.

2. The variation among different matings in respect of reproductive index is relatively large, as shown by the standard deviations and coefficients of variation. It is similar in this respect to variation in other physiological, as contrasted with structural, characters (PEARL 1905). In the present case this high variability is certainly only what would be expected, since the value taken by the reproductive index depends on the interaction of a series of physiological factors or processes, each of which is rather highly variable taken by itself.

3. Turning to the question of the effect of age upon the reproductive index we see that, having due regard to probable errors and the number of matings involved, *the highest mean value of the index in the case of these Barred Plymouth Rock matings is found when sire and dam are each one year old at the time of the mating.* The only higher mean in the table is that for sire = 1, dam = 3, and in that case only 7 matings are available, a number far too small to base a result upon.

The fact that the net reproductive results with cockerels and pullets are superior to those with older birds is directly contrary to the teaching of most of the poultry authorities. It is usually taught that the eggs of pullets are very apt to be infertile, and that the chicks which are obtained will be greatly lacking in vitality. The only recent writer I have found who does not subscribe strongly to such views is ROBINSON (1912), and even he inclines a little to the notion that, even though cockerel—pullet matings do produce a more numerous progeny than matings of older birds, the offspring of the younger birds may lack in "quality." "Quality" is an elusive term, not capable of numerical, quantitative statement. What the present statistical data show is that on the basis of the chick's *ability to live* as an index of constitutional vigor and vitality (and the writer's ten years experience with poultry has

shown him no better index of these qualities than this same ability to live) the net reproductive results are on the average *superior*, in the case of the MAINE STATION Barred Rock stock, when the parents are from 10 to 14 months of age at the time when the matings are made than if they are older. Whether or not this same relation holds for other breeds, or strains, and methods of management is a matter of great practical as well as theoretical interest. At present the writer knows of no reliable quantitative data sufficient in amount to base an opinion upon regarding this point.

4. Upon the question of the relative changes of the two sexes in reproductive ability, with advancing age, the following weighted mean figures for *males* may first be examined. The weighting in each case is in proportion to the number of matings involved, as indicated in table 2.

Weighted mean reproductive indices for males of specified ages mated with females of all ages.

Ages						Weighted mean RI
Male = 1,	mated	with	♀	♀	of all ages	12.868
Male = 2,	"	"	"	"	"	10.214
Male = 3,	"	"	"	"	"	9.625

Similar figures for *females* may next be examined.

Weighted mean reproductive indices for females of specified ages mated with males of all ages.

Ages						Weighted mean RI
Female = 1,	mated	with	♂	♂	of all ages	12.765
Female = 2,	"	"	"	"	"	11.660
Female = 3,	"	"	"	"	"	11.455

These data are shown graphically in fig. 2.

From these figures it appears clearly that there is a decline in net reproductive ability, as measured by the reproductive index, with advancing age in both sexes. The rate of the decline is, however, more rapid in the male than in the female. This result is what might reasonably be expected in a polygamous animal such as the fowl. A single male mates with a number of females, and in addition is much more active, on the whole, than the females, what with fighting, looking after his flock, etc. The writer judges it to be the experience of poultrymen generally that it is much more difficult to keep a cock bird in good condition for breeding at an advanced age than it is so to keep hens.

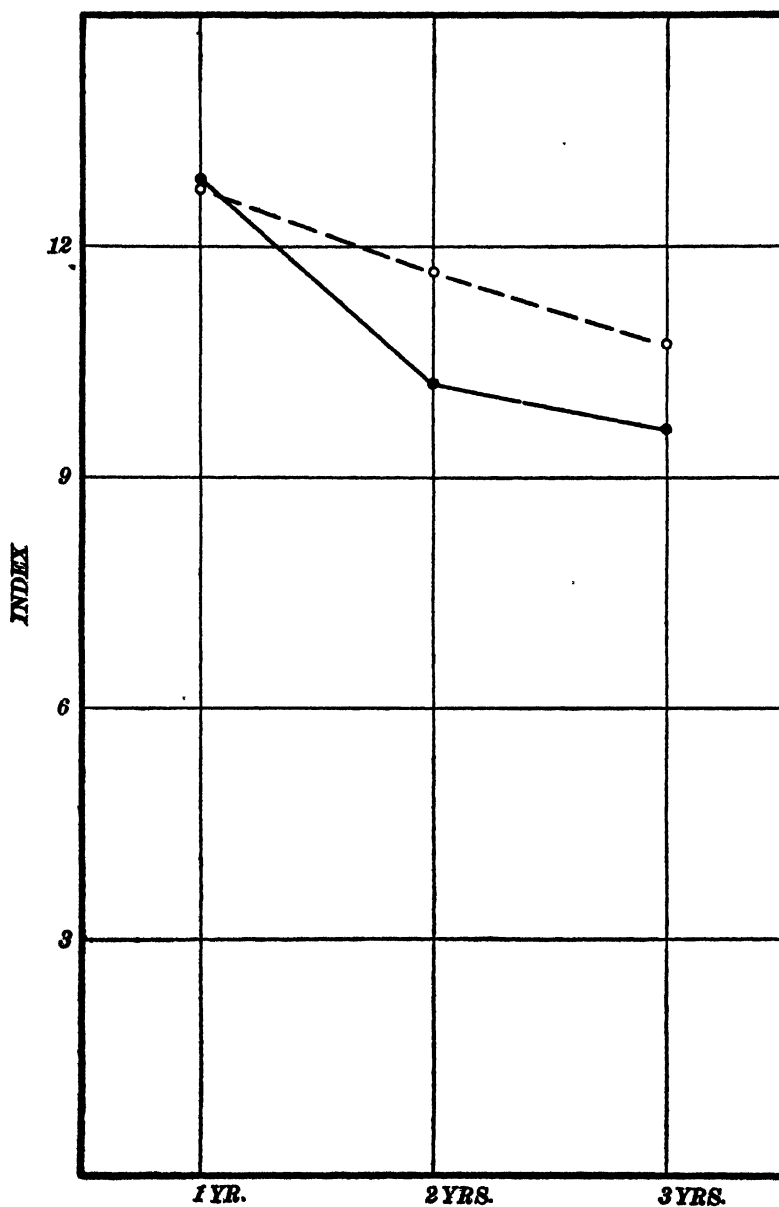


FIGURE 2.—Showing the change in reproductive index with advancing age, for males and females. Solid line and circles = males; broken line and open circles = females.

5. In the preceding section we have considered the change in reproductive ability with age in the sexes separately. It is desirable also to look at the matter from the standpoint of the *mating*. This may be done by taking means (weighted in proportion to the frequencies in-

volved) of the reproductive indices for the advancing ages of the two animals entering into each class of matings as given in tables 2 and 3. If this is done we get the following results.

Weighted mean reproductive indices for matings of individuals of the specified combined ages.

Combined ages of mated individuals when mated	Cases	Weighted mean RI
2 years	796	13.083
3 years	190	11.121
4 years	113	11.119
5 years	12	7.458
6 years	3	15.667

The cases are too few to give reliable results after a combined age of 4 years. Up to that point, however, what occurs is this: there is a significant drop in reproductive ability as we pass from a combined age of 2 years for the mated birds to 3 years. In passing from 3 years to 4 years there is no significant change in reproductive ability. In passing from a combined age of 4 years to that of 5 years there is a large drop in the net reproductive ability of the mating. The number of matings where the combined age was 5 years is, to be sure, small and too great dependence is not to be put upon the mean. It is however highly probable that there is some drop in reproductive ability at this point, though it may not be so great in amount as is indicated by the present figures. The number of cases of matings with a 6 year combined age is altogether too small to have any meaning whatever. Taken as a whole the present figures bear out very well the conclusion already reached that, for the strain of birds and the environmental conditions here dealt with, the highest net reproductive ability is found in birds one year old (cock-erels and pullets) at the time they are mated.

The combined age means are shown graphically in fig. 3.

DISCUSSION

The most significant general result of the present study is the new index proposed for the measurement of the net reproductive ability of matings of the fowl. An adequate measure of this character has been much needed, and opens out the way to the attack on a number of problems. Such questions as the relation of reproductive ability to breed and variety, to the long-continued administration of drugs such as alcohol, ether, etc., to inbreeding, and the degree of heterosis, and many

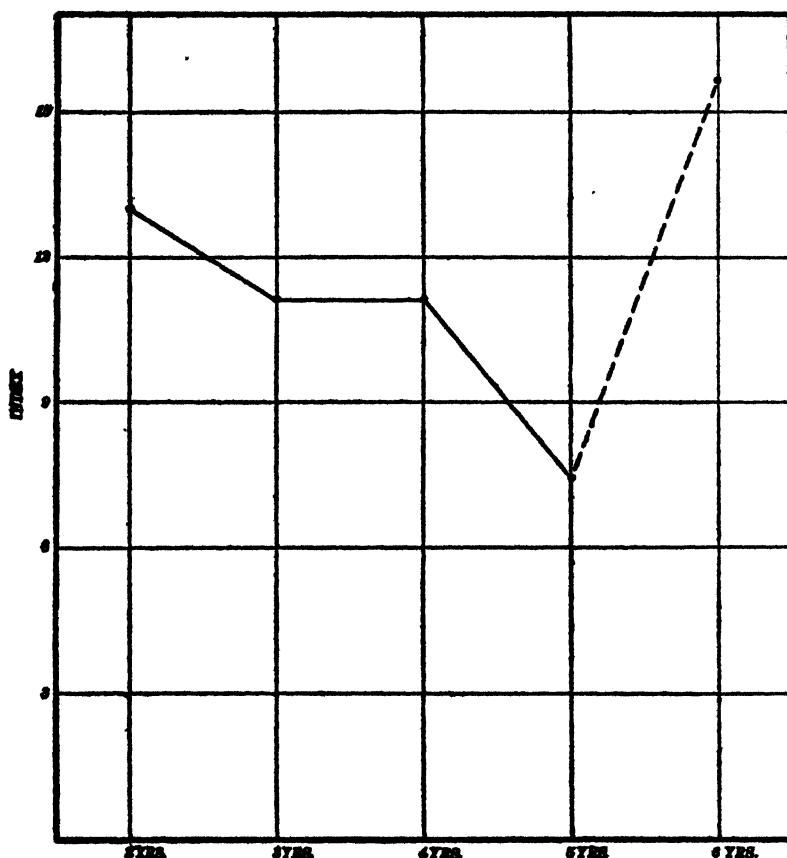


FIGURE 3.—Showing the change in reproductive index with advancing combined ages of the mated individuals. The dotted line signifies that in this region of the graph the data are too few to give reliable results.

other similar problems may now be profitably attacked. The writer hopes to return to the discussion of some of these problems in later papers. It is important that one caution be observed in applying this new reproductive index in the treatment of general problems. It is necessary that the duration of all matings compared in respect of reproductive index be substantially the same. The reason for this is that the value of the index will be somewhat affected by the length of time covered by the mating. Of course, in ordinary breeding practice this condition will be realized usually, but it will be well to keep the point in mind in making use of the index.

The character which has been called "reproductive ability" is practically the same thing as "fertility" as defined by PEARL and SURFACE

(1909 a). The only essential difference is that here the ability of the offspring to live is taken into account, whereas in the earlier definition fertility was taken to mean only bringing to birth. On the whole it seems now that the underlying idea of the present paper gives a more adequate and useful conception of fertility than the earlier one. We might then define fertility as the total net reproductive capacity of pairs of organisms, male and female, as indicated by their ability to produce *viable* individual offspring. As a working measure of fertility may be taken a reproductive or fertility index which expresses the percentage which the number of viable offspring actually produced from a particular mating or pair of parents is of the maximum number which would be physiologically possible within the time limits during which the mating endures. This states in most general terms the form of index developed in this paper for the special case of poultry breeding. The same idea can be adapted to the measurement and biometrical study of fertility in other sorts of animals, and probably in plants as well.

Turning to the special problem with which this paper deals, the influence of age upon the fertility of matings of the fowl, we find that for the strain of Barred Plymouth Rocks and the environmental conditions here dealt with, maximum reproductive capacity is, on the average, attained in both sexes in the first breeding season. Never after that is the average fertility (as above defined) so high. It is of course to be understood that the pullets and cockerels involved in these statistics, and on the basis of which the above statement is made, were well matured birds, in no case less than 10 months old when mated, and from that to 14 months. Sexual maturity, as evidenced by the physiological ability to produce offspring, is regularly attained at an earlier age than this, and occasionally at a very much earlier one. The writer has in his possession now a brood of chicks, the *combined* ages of whose parents amounted to only one year. They are small and inferior birds. It is undoubtedly in considerable part as a result of breeding from such very young birds that the prejudice against the use of pullets and cockerels as breeders at all has arisen among poultrymen, and led to such statements in the texts as the following from LEWIS (1913):

"When pullets are used as breeders, a large percentage of the eggs set are infertile, undoubtedly as a result of immaturity. The chicks at hatching time and maturity prove to be small."

There are undoubtedly a number of factors concerned in the decline of net reproductive capacity after birds have passed the first breeding

season. One important one is that emphasized by ROBINSON (1912) who says:

"It is largely a question of condition. The older a bird grows, the more difficult it is to keep it in good breeding condition. Few fowls and ducks are as good breeders the third year as the second, fewer still are good after the third year; yet occasionally four- and five-year-old birds of both sexes will breed as well and the hens lay as well as young stock, and there are authentic instances of fowls breeding well at seven and eight years of age."

MARSHALL (1908) has shown that general environmental conditions, nutrition, etc., may affect fertility in mammals. Besides these external factors in the decline there are also, without question, important internal factors operating in the same direction. VON HANSEMAN (1913) and KÄPPEL (1908) have shown that there is a progressive diminution of oöcytes in the ovary with advancing age. The analysis of the relative importance of these various factors in changing fertility is a problem of the future. It is believed that the possession of a simple and adequate measure of net fertility will aid materially in the study of this problem.

SUMMARY

1. A new constant, the reproductive or fertility index, is proposed for the measurement of the net reproductive ability of mated pairs of the domestic fowl.
2. This index expresses the actual number of chicks produced by the mating and capable of living three weeks after hatching as a percentage of the maximum total number of chicks which it would be physiologically possible for the mating to produce during the time which it endures, each of these theoretical chicks being supposed to live to at least three weeks of age.
3. The values of this reproductive index are calculated for 1114 Barred Plymouth Rock matings, covering a period of nine years, and the data so obtained are treated biometrically.
4. For the strain of Barred Rocks used, and under the conditions of environment and management which obtained during the experiments, the reproductive index has a mean value of about 12 percent.
5. Net fertility, as measured by the reproductive index, is a rather highly variable character, agreeing in this respect with other purely physiological characters.
6. Reproductive ability, as measured by the index, diminishes with advancing age of the birds mated, having its maximum when each of the birds mated is from 10 to 14 months of age.

7. The decline in reproductive ability with advancing age is at a more rapid rate in the case of the males than in the case of the females.

8. The results above stated are to be understood as being limited, for the present, to the breed, strain, and circumstances, which furnished the data. How wide their generality may be is a matter yet to be investigated.

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THE RELATION OF YELLOW COAT COLOR AND BLACK-EYED WHITE SPOTTING OF MICE IN INHERITANCE

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CUÉNOT, STURTEVANT and MORGAN have all shown that a series of mutually allelomorphic forms of coat pattern exists in mice. There are four types of pattern in this series. These in order, from the most hypostatic to the most epistatic, are as follows: (1) *Non-agouti*, the ordinary "self" or "unticked" coat pattern. (2) *Agouti* or better *gray-bellied agouti*, the coat pattern seen in the ordinary wild house mouse. (3) *White-bellied agouti*, in which there is a decrease in brown and black pigmentation resulting in more yellow on the dorsal surface and white-tipped ventral hairs. (4) The final member of the series, the *yellow* coat pattern in which almost, if not all, the brown and black pigment of the coat has disappeared and is replaced by yellow.

It is easy to obtain mice homozygous for any of the three lower members of the series: non-agouti, gray-bellied agouti, and white-bellied agouti. No one, however, has yet obtained yellow mice which are homozygous. There is every reason to believe that the process of fertilization between two yellow-bearing gametes occurs (CASTLE and LITTLE 1910). The ratio of yellow to non-yellow young, however, makes it certain that the homozygous yellow zygotes do not reach a sufficiently advanced age to enable one to record them (CASTLE and LITTLE 1910, LITTLE 1911, DURHAM 1911, DUNN 1916). The size of litters when yellows are crossed *inter se* is also smaller than when yellows are crossed with any of the hypostatic types (CASTLE and LITTLE 1910, DURHAM 1911, DUNN 1916).

If we are to consider that allelomorphs occupy the same locus in the chromosome we are faced with a condition somewhat as follows. Four distinct stages occur in the restriction of brown and black pigment from the coat. The first three stages, though they cover a wide range of variation in extent of brown and black pigmentation, may all of them be obtained in a homozygous condition. The fourth step, however,

apparently so affects the individual that it can exist only when balanced in the zygote by one of the three lower steps. When both gametes contain the factor for this advanced restriction, the zygote perishes early in its existence.

In a most interesting paper given at the recent New York meeting of the AMERICAN SOCIETY OF ZOOLOGISTS, KIRKHAM has reported the discovery of disintegrating embryos in mice, where the "homozygous yellow" embryos should be found. These disintegrating embryos occur in number corresponding sufficiently well with the Mendelian expectation to make the evidence concerning the fate of the homozygous yellow zygote conclusive.

It is also of fundamental importance to note that in this case, a color factor has shown that it may be an active force in morphogenesis long before the embryo has formed any pigment whatever. This indicates clearly that *the function of a genetic factor may be entirely different at different stages in ontogeny.*

A similar condition exists in the case of "black-eyed white" spotting in mice. Independent in inheritance of either self coat or the ordinary piebald spotting, the black-eyed white factor produces, when acting on "self" mice, an individual with a small number of white spots, occasionally irregular in outline, and when acting on piebald mice, a white individual with pigmented eyes. Such black-eyed whites, however, do not breed true, but give a ratio of approximately one piebald to two black-eyed whites, when crossed *inter se* (LITTLE 1915).

Since these two peculiar results in mice stand as entirely distinct from any others obtained in the study of color factors in rodents it seemed worth while to investigate what relation, if any, they bear to one another.

For the purposes of explanation we may construct the following diagrams to show the separate behavior of the "yellow" and the "black-eyed white" factors in heredity.

Let Y equal the factor for "yellow" coat pattern, and y equal that for non-yellow (non-agouti, gray-bellied agouti, or white-bellied agouti, as the case may be). A heterozygous yellow may be represented by the factors Yy . Such an animal forms gametes Y and y . When two such yellows are crossed together, the following result is obtained:

Mating, $Yy \times Yy$

Gametes, Y and y Y and y

Zygotes, 1 YY , homozygous form which fails to continue development.

2 Yy , heterozygous yellow.

1 yy , non-yellow.

Similarly we may let W equal the factor for "black-eyed white" spotting, and w its absence. A heterozygous black-eyed white mouse would have the formula Ww . If two such animals were crossed *inter se* the following result would be obtained:

Mating, $Ww \times Ww$

Gametes, W and w W and w

Zygotes, 1 WW , homozygous form which fails to develop.

2 Ww , heterozygous black-eyed whites.

1 ww , non-black-eyed white (ordinary piebald).

The interesting question to answer, if possible, is whether Y and W act in an identical manner and therefore are unable to exist in a single zygote. Further, if they are not identical, are they in any way related or are they entirely distinct physiologically and genetically.

All the "black-eyed white" mice used in the earlier experiments with this variety were non-yellow; i. e., gray-bellied agouti or non-agouti. This was shown by the fact that all of the piebald young produced by them were either gray-bellied agouti or non-agouti. We may then express the zygotic formula of the black-eyed whites as follows: yyH^w , that is to say they were homozygous for "non-yellow" but heterozygous for the "black-eyed white" factor. The yellows used were entirely free from the "black-eyed white" factor and of course possessed the yellow factor in a heterozygous condition. Their formula would be $Yy\alpha w$. A cross between yellow and black-eyed white (non-yellow) mice would give the following result:

Yellow, $Yy\alpha w \times yyH^w$, black-eyed white (non-yellow)

Gametes, $Y\alpha$ and $y\alpha$ yH and $y\alpha$

F_1 zygotes, (a) YyH^w , yellow.

(b) $Yy\alpha w$, yellow.

(c) yyH^w , non-yellow.

(d) $yy\alpha w$, non-yellow.

If the lethal action of Y and W is the same, the YyH^w individuals comprising class (a) of the F_1 generation should be non-viable. The $Y\alpha$ and yH gametes might meet in fertilization, just as do two Y or two W gametes, and the resulting zygote might perish before attaining sexual maturity as do the YY and WW zygotes. If this happened, class (a) of the F_1 generation would form but fail to develop and the resulting ratio of yellow to non-yellow young in F_1 would be one to two, not one to one. The actual numbers of F_1 young observed were, yellows 76, non-yellows 81. On a 1 : 1 ratio the Mendelian expectation would be 78.5 : 78.5. If a 1 : 2 ratio was the correct explanation the numbers expected are

52 yellow, 105 non-yellow. There is no doubt that the equality ratio is the one approximated. This being the case, it is certain that the action of y and W is not identical.

The next matter of interest is to determine whether *any* relationship between Y and W exists, or whether they are entirely distinct from one another.

One possibility is that no fusion between a Yw and a yW gamete is possible. There might be a selective fertilization. If this is the case, the Yw gametes would always be met in fertilization by yw gametes producing Yyw zygotes. The yW gametes will always fertilize or be fertilized by yw gametes producing yyW zygotes. *The result would be that F_1 yellow animals when crossed inter se or with piebald mice of any color should never give black-eyed white young.* The F_1 ratio would probably approximate one yellow to one non-yellow and we should have to resort to a breeding test and an F_2 generation to determine whether or not there was actual selective fertilization. As a possible modification of this idea of selective fertilization one might imagine that the combination $YyWw$ rarely did form but that would mean that an occasional yellow F_1 animal would carry the W factor and give rise to black-eyed white young, when suitably mated. The exact ratio of such yellows to the more common Yyw type would be determined by the degree of antagonism between Yw and yw gametes which had to be overcome before their union was possible.

The remaining hypothesis is that Y and W although they act alike in their elimination of a zygote containing a double dose of either of them, are physiologically and genetically entirely distinct. If such were the case, the F_1 generation would have an equality ratio of yellows to non-yellows and approximately an equal number of *each* color would or would not carry the W factor.

Before turning to the experimental evidence on which the tests of these hypotheses are based, it may be profitable to review very briefly the main facts of the genetic behavior of black-eyed white mice. When black-eyed whites are crossed with self-colored, non-yellow mice, two sorts of F_1 animals are obtained. These I have described and figured in a previous paper (LITTLE 1915). I have called them type A and type B. Type A has a distinct spotted appearance. The head and hind quarters are commonly pigmented, but the trunk is usually unpigmented to a considerable degree. The spots of pigment in this position of the body are inclined to be small and irregular in outline in

contrast to the large and regular type of pigment patch seen in piebald mice and guinea-pigs. Type B is either entirely without white or else possesses a small amount of white on the ventral surface. Mice of this type are indistinguishable from the heterozygotes obtained when self-colored and piebald mice are crossed.

The type A animals all of them carry the W factor and produce a certain number of black-eyed white young when crossed *inter se* or with piebald animals. The type B animals never give black-eyed white young when crossed *inter se* or with piebalds. The actual numbers which I have obtained are as follows. These figures are a combination of those already reported (LITTLE 1915) with additional data from new crosses between self-colored dilute brown and black-eyed white (non-yellow) mice.

Black-eyed white \times *self-colored*:

F_1 generation: Type A, 91, type B, 98.

Type A \times *piebald*:

Observed: Self-colored, 64; type A, or spotted, 96; black-eyed white, 42.

Expected: 50.5 101.0 50.5

Type B \times *piebald*:

Observed: Self-colored or type B, 94; piebald, 101.

Expected: 97.5 97.5

If we represent the factor for black-eyed white spotting by W and its absence by w , and the factor for self coat by S and its allelomorph for piebald coat by s^p , we may represent the above-mentioned crosses as follows:

Mating: Black-eyed white $s^p s^p W w$ \times $SS w w$ self-colored (non-black-eyed white)

Gametes: $s^p W$ Sw
 $s^p w$ Sw

F_1 zygotes $Ss^p W w$, type A.

$Ss^p w w$, type B.

Type A \times piebald

$Ss^p W w \times s^p s^p w w$

$\left. \begin{array}{l} SW \\ Sw \\ s^p W \\ s^p w \end{array} \right\} s^p w \text{ gametes}$

Zygotes $\left\{ \begin{array}{l} Ss^p W w, \text{ type A} \\ Ss^p w w, \text{ self or type B.} \\ s^p s^p W w, \text{ black-eyed white.} \\ s^p s^p w w, \text{ piebald.} \end{array} \right.$

Type B \times piebald

$Ss^p w w \times s^p s^p w w$

$\left. \begin{array}{l} Sw \\ s^p w \end{array} \right\} s^p w \text{ gametes}$

Zygotes $Ss^p w w$, type B
 $s^p s^p w w$, piebald.

EXPERIMENTAL EVIDENCE FROM CROSSES BETWEEN YELLOWS AND BLACK-EYED WHITE MICE

In making these matings reciprocal crosses were made and gave identical results. Generally speaking it may be said at the outset that the F_1 generation animals possessed much less white than the F_1 animals in either of the former crosses between black-eyed white and self-colored mice. If the F_1 animals are classified into type A and type B mice according to previous methods the yellow \times black-eyed white matings gave only 63 type A to 94 type B instead of the expected equality ratio of 78.5 to 78.5. If we analyze this generation more closely we find that among the non-yellow animals of the F_1 generation, there is an almost absolute equality of type A and type B animals. The exact figures are forty-one non-yellow type A and forty non-yellow type B. The yellow F_1 animals, however, give a decided preponderance of animals with no dorsal white, which are classed as type B. The actual figures in the yellows are twenty-two of type A and fifty-four of type B. Superficially the evidence appears to favor the idea of selective fertilization. A study of the F_2 generation, however, brings out certain extremely interesting facts which make any such assumption unnecessary.

If the type B animals obtained in the F_1 generation of the yellow—black-eyed white cross be tabulated according to the approximate percentage of the ventral surface which is unpigmented it will be noticed that many of the *yellow* type B animals have a distinctly greater amount of unpigmented ventral surface than do the type B non-yellows obtained in the same crosses.

Generation		Percentage of ventral surface white																	
		0	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	—	—	—	76-90	Total
F ₁ yellow	Type B	29	8	8	2	3	1	0	0	1	0	1	0	0	0	0	0	1	54
F ₁ non-yellow	Type B	31	8	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40

Thus thirty-nine of the forty or 97.5 percent of the non-yellow type B animals have less than 6 percent of the ventral surface white while only one has just 6 percent. On the other hand among the yellow type B mice seventeen or 31.4 percent have 6 percent or more of the ventral surface white. Nine of these or 16.6 percent of the total yellows have a degree of whiteness not recorded in type B animals of any previous cross. Eleven of the seventeen yellow animals showing 6 percent or more ventral white have been tested by crossing *and have all shown that they are really type A individuals, not type B as they had been*

classified. If we remove these from the latter category and place them under type A where they really belong, we have the following result:

	Before correction	After correction	<i>Expected</i>
Yellow type A	22	33	39
Yellow type B	54	43	39
Non-yellow type A	41	41	39
Non-yellow type B	40	40	39

There is every reason to believe that if the other six yellows of a similar degree of whiteness to those tested had also been bred, a further addition to the yellow type A class and subtraction from the yellow type B class would be made, thus bringing the figures even closer to the expected results.

The corrected figures suggest that the proper hypothesis is one of complete independence between the factors for yellow and black-eyed white.

TEST MATINGS OF F_1 ANIMALS

Non-yellow type A animals of the F_1 generation were tested by crossing them with piebald mice. The details of such a cross have already been worked out above. The expectation is one piebald to one type A, to one self-colored or type B, to one black-eyed white. Classing the first two named types together, since at times no distinguishing breeding tests were made, we should expect two spotted, to one self-colored or type B, to one black-eyed white. The actual result was:

	Observed	<i>Expected</i>
Spotted	22	22
Self or type B	10	11
Black-eyed white	12	11
Total	44	44

The agreement between observation and expectation is striking. Yellow type A animals, among which the eleven tested mice first classed as type B are included, have been crossed with piebald non-yellows and have given a total of 165 young. The classes of young expected in this cross are exactly the same as in the previous cross with the exception that there is an equal chance of an animal being yellow or non-yellow in

color. The ratio expected then, is one self yellow or type B, to one black-eyed white (yellow), to two spotted yellows, to one non-yellow self or type B, to one black-eyed white (non-yellow) to two non-yellow spotted. The actual results follow:

	Observed	<i>Expected</i>
Yellow spotted	35	42
Non-yellow spotted	46	42
Yellow self or type B	31	21
Non-yellow self or type B	21	21
Yellow black-eyed white	4	21
Non-yellow black-eyed white	28	21
Total	165	168

If we tabulate this generation in a slightly different way we find that the expected figures are approximated more closely in the non-yellows than in the yellows.

	Yellow		Non-yellow	
	Observed	<i>Expected</i>	Observed	<i>Expected</i>
Spotted	31	34	46	48
Self or type B	35	17	21	24
Black-eyed white	4	17	28	24
Total	70	68	95	96

It is possible by a close examination of the yellow animals to re-classify certain animals on the basis of comparison with the F_1 generation and of direct breeding tests. Thus there are among the thirty-one yellows of the self or "type B" class, eleven which are identical in appearance with the F_1 "type B" yellows that upon breeding turned out to be type A. While all eleven have not been tested by breeding, several have, and seem to justify classifying these eleven animals under the spotted category as being type A in genetic constitution. After this change the figures read:

	Before change	After change	<i>Expected</i>
Yellow spotted	35	46	34
Yellow self or type B	31	20	17
Yellow, black-eyed white	4	4	17

The discrepancy between the observation and expectation in the yellow black-eyed white class is interesting but I believe only apparent. If the yellow and non-yellow spotted animals are tabulated according to the percentage of the dorsal surface which is pigmented it will be noticed that there are fourteen yellows that have less pigment than all but two of the non-yellow spotted mice. Ten of them have less than thirty per-

Generation	Percentage of dorsal surface pigmented									Total
	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-99	
Yellow spotted F_2	8	2	1	3	1	3	3	7	8	36
Non-yellow spotted F_2	1	0	1	0	4	10	6	11	9	42

cent of the dorsal surface pigmented and eight have twenty percent or less. Ordinarily non-yellow black-eyed whites have, as I have shown in my earlier paper, rarely more than 5 percent of the dorsal surface pigmented. Since, however, certain of the F_1 and F_2 type A yellows have distinctly more pigment than the corresponding variety of non-yellows, it seemed probable that the same might hold true in the case of yellow and non-yellow black-eyed whites. In order to test this question, several of the lightly pigmented spotted yellows were bred to non-yellow piebald mice. The uniform result when yellows with twenty percent or less of dorsal pigmentation are crossed with piebalds was the production of a nearly equal number of black-eyed white¹ and piebald young. This proves that they are genetically black-eyed white mice and are not, therefore, to be included in the "spotted" column. We may then properly remove the yellows with twenty percent or less dorsal pigmentation from the spotted class and place them in the class of yellow black-eyed whites as follows:

	Before change	After change	Expected
Yellow spotted	46	38	34
Yellow self or type B	20	20	17
Yellow black-eyed white	4	12	17
Total	70	70	68

Undoubtedly the separation of yellows at the twenty percent mark is arbitrary and it is certain from breeding tests of lightly spotted yellows of other more advanced generations that animals with as much

¹ Among the black-eyed whites are classed yellows resembling their parents, i. e., with 5-20 percent of the dorsal surface pigmented.

as forty percent of the dorsal surface yellow may breed like black-eyed whites. This means that if breeding tests had been made of the two yellows with between twenty and thirty percent dorsal pigmentation both of them would in all probability have joined the class of black-eyed whites and brought the figures even closer to the expectation.

We may now combine the yellows and non-yellows in one category, according to whether they are spotted, black-eyed white, or belong to the self type B class. When this is done the following figures are obtained:

	Observed	<i>Expected</i>
Total spotted	84	82
Total self type B	41	41
Total black-eyed white	40	41
Grand total	165	164

Breeding tests of yellow type B animals crossed with piebald non-yellows show that, as expected, they give four classes of young,—yellow and non-yellow self or type B and piebald yellows and non-yellows in approximately equal numbers.

	Observed	<i>Expected</i>
Yellow self type B	36	35
Non-yellow self type B	37	35
Yellow piebald	30	35
Non-yellow piebald	38	35
Total	141	140

Non-yellow type B animals crossed with piebald give essentially similar results, the yellow classes are, of course, lacking.

	Observed	<i>Expected</i>
Non-yellow self type B	43	36
Non-yellow piebald	29	36

Breeding tests of the back-cross animals produced in the above crosses have shown that all of the expected genetic classes of young occur. In view of this fact it appears fairly certain that the test of the relationship of the yellow and black-eyed white factors has been satisfactorily made.

SIZE OF LITTERS

CASTLE and LITTLE (1910) have called attention to the fact that litters from yellow \times yellow matings are smaller on the average than litters from yellow \times non-yellow matings. If the given explanation of the relationship of the yellow and black-eyed white factors is correct the litters produced by crossing together two yellow type A mice should be distinctly smaller than the litters produced when a yellow type A mouse is crossed with a piebald non-yellow. The reason for this will become apparent if we examine the types of zygotes formed when two yellow type A animals are intercrossed.

Mating: Yellow type A $YyW'w \times YyW'w$ yellow type A

Gametes: $YW' \ YW'$
 $Yw \ Yw$
 $yW' \ yW'$
 $yw \ yw$

Zygotes as shown by the checker-board method.

	YW'	YW'	yW'	yW'			
1	YW'	2	Yw	3	yW'	4	yw
	Yw	Yw	Yw	Yw			
5	YW'	6	Yw	7	yW'	8	yw
	yW'	yW'	yW'	yW'			
9	YW'	10	Yw	11	yW'	12	yw
	yw	yw	yw	yw			
13	YW'	14	Yw	15	yW'	16	yw

Any zygote containing two "doses" of either the Y factor or the W factor is eliminated. This would remove zygotes Nos. 1, 2, 3, 5, 6, 9, and 11. Only nine of the sixteen original combinations can continue development and this would result in cutting the litters to nearly one-half their expected size. What actually happens may be seen from the following figures. Ten litters from yellow type A parents crossed *inter se* gave a total of thirty young or an average of three per litter. On the other hand nine litters of young produced by crossing yellow type A mice with non-yellow piebalds produced forty-five young or an average of five per litter. The figures though not extensive bear out the explanation of the relationship of the two factors as outlined above.

INCREASE OF PIGMENTATION IN YELLOW MICE

The fact that yellow type A and black-eyed whites potentially yellow

have considerably more pigment than the corresponding non-yellow varieties in the F_1 and F_2 generation suggests that the increase may be due to a darkening factor which coming in apparently with the Y -bearing gamete of the yellow race shows a marked tendency to remain coupled with yellow coat color in inheritance. Experiments have been started to determine whether the increased pigmentation of yellow animals is due to interaction of factors or to linkage of a darkening modifier as suggested above.

CONCLUSIONS

(1) The factors for yellow coat color and for black-eyed white spotting in mice are both physiologically and genetically distinct and independent from one another.

(2) Certain apparent indications of selective fertilization and abnormal Mendelian ratios are found not to hold after breeding tests of the animals in question have been made.

(3) Yellow F_1 animals of "type A" are distinctly more heavily pigmented than non-yellow animals of the same type and generation.

(4) "Black-eyed whites," potentially yellow, have from 6-20 percent more dorsal pigmentation than do the corresponding black-eyed whites potentially non-yellow.

(5) Until further evidence is collected, this increase in pigmentation may be considered as due either (a) to a modifying factor linked with yellow or (b) to an interaction between the factor Y' and the factor W' of a purely somatic nature.

(6) Litters produced from yellow "type A" parents crossed *inter se* are distinctly smaller than litters in which only one parent is of this variety. This reduction is probably due to the formation and subsequent death of zygotes having a double representation of either the Y or W factor or of both.

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DEFICIENCY¹

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INTRODUCTORY SUMMARY

The general term "deficiency" is used to designate the loss or inactivation of an entire, definite, and measurable section of genes and framework of a chromosome. A case of deficiency in the X chromosome of *Drosophila ampelophila* occurred in September 1914, and has given rise to a whole series of correlated phenomena.² The first indication of this deficiency was the occurrence of a female which had failed to inherit from her father his sex-linked dominant mutant "bar",³ though she inherited in a normal manner his sex-linked recessive mutant "white." This female, when bred, gave only about half as many sons as daughters, the missing sons, as shown by the linkage relations, being those which had received that X which was deficient for bar. This lethal action in-

¹ Contribution from the Zoölogical Laboratory of COLUMBIA UNIVERSITY, and the CARNEGIE INSTITUTION OF WASHINGTON.

² A brief account of deficiency was included in "Non-disjunction as proof of the chromosome theory of heredity." *Genetics* 1: 1-52, 107-163, Jan.-Mar., 1916. A fuller account was read before the American Society of Naturalists at the meeting held at COLUMBIA UNIVERSITY on December 29, 1916.

³ For information about the various mutants, and for an explanation of the terms and symbols used, see appendix, p. 456.

icates that the deficiency mutation involved not simply the bar, but was also a deficiency for one or more genes necessary to the life of the fly. It was next found that the deficiency was extensive enough so that it included the locus for "forked," a recessive mutant whose gene lies in the X chromosome about half a unit from the locus of bar. A deficient-bearing female behaves as though haploid for forked, so that a $\frac{\text{---}}{f}$ female is forked although forked is a strict recessive. That the region between forked and bar was likewise affected, was demonstrated by the disappearance of crossing over between these loci in females having a deficient X. The deficiency mutation is thus proved not only to have affected a region of adjacent genes but also to have affected the framework of the chromosome on which crossing over must primarily depend. The maximum and the minimum lengths of the deficient region were measured by two genetic methods—by means of haploid tests and by means of linkage. The length of the chromosome as tested by linkage was found to be shorter than normal by an amount corresponding to the length of the deficient region. Unfortunately the stock of deficiency was lost before a cytological examination was made. The fact that the female with one X deficient for bar and the other X carrying bar ($\frac{\text{---}}{B'}$) is an intermediate like the normal bar heterozygote, leads to the conclusion that the intermediate eye shape is due to the broadening action of genes outside the bar locus rather than to a broadening action of the normal allelomorph of bar (b'). Of the two alternative explanations of the nature of deficiency, viz., physical loss and complete inactivation, the loss view is perhaps slightly favored by the evidence. The origin of the dominant mutant bar can not be explained on the "presence and absence" hypothesis as due to the loss of an inhibitor, for the loss of the inhibitor region through deficiency does not give a result comparable to the bar mutation. Sex differentiation was not affected by the occurrence of deficiency; hence sex is determined by specific differentiators which are in some part of the X other than the region from forked to bar. This case of deficiency enables us to establish an identity between the actual localization of certain genes in the X chromosome and their positions as mapped by means of linkage.

THE OCCURRENCE OF THE DEFICIENCY FOR BAR

The exception which led to the discovery of the first case of deficiency occurred (September 25, 1914) among the offspring of an XXY wild-

type female heterozygous for eosin and for vermilion ($\frac{w^e}{v}$) which had been outcrossed to a white bar male ($\frac{w}{B'}$) of a pure stock (table 1). Bar is a dominant mutant, for which reason all

TABLE 1

The occurrence of the bar-deficient exception among the offspring of a $\frac{w^e}{v}$ ♀ outcrossed to a white bar. ♂.

No.	Regular ♀ ♀		Regular ♂ ♂				Exceptions by secondary non-disjunction		Exception by bar-deficiency
	$w-w^e B'$	B'	$\frac{w^e}{v}$	v	$w^e v$	v	+	+ ♀	$w B' \delta$
546*	60	59	45	48	14		18	10	10
									1

* This culture appeared in table 9, p. 23, of "Non-disjunction as proof of the chromosome theory of heredity," *Genetics* 1: Culture 546 is not included in the summary of table 14, appendix.

the daughters were bar,—either white-eosin bar ($\frac{w^e}{w} \frac{B'}{B'}$) or simply bar ($\frac{v}{w} \frac{B'}{B'}$),—except one, which was white-eosin but *not* bar ($\frac{w^e}{w}$). That is, *she had inherited the white from her father but had not inherited his bar*. If the genes for all the sex-linked characters are transmitted to daughters by means of a common vehicle, viz., the single X chromosome, then so long as this X is intact and behaves as a unit there should be no chance for him to transmit some of his sex-linked characters without transmitting all of them, as occurred in this case.

The mutation responsible for the bar-deficiency occurred in the germ tract of the white bar male at or close to the maturation division; for he produced many regular daughters but only one with the bar gene deficient.

THE LETHAL ACTION OF DEFICIENCY

The white-eosin exceptional daughter, outcrossed to a wild male, gave (table 2) no bar offspring whatever,—a fresh proof of the deficiency of bar. The sons were of the two expected classes, eosin and white; white was thus again proved to have been transmitted. But the total of the

TABLE 2

The lethal result given by the white-eosin bar-deficient female of culture 546 when outcrossed to a wild male.

Culture	Daughters	Sons			
		$\frac{w}{w^e}$	—	$\frac{w}{w^e}$	—
No.		Dies	w^e	w	Dies
593	84	—	37	14	—

sons (51) was only about half the total of the daughters (84), and the white sons (14) were much fewer than the eosin (37). The culture which produced the bar-deficient exception (table 1) contained no such lethal, as is shown by the equality of the sexes (130♀:135♂) and by the equality of all contrary classes. The appearance of an inequality of sexes and of contrary classes indicates that whatever cause had removed or transformed the bar of the white bar chromosome was sufficiently damaging so that every male which received the deficient chromosome was unable to come to maturity. The deficiency was then not simply for bar but was also a deficiency for one or more genes whose normal action is essential to the life of the fly. The amount of linkage shown between the lethal effect and white is that expected on the view that the lethal change occurred at or near the bar locus. The white sons which did live were those which by crossing over in the mother ($\frac{w^e}{w}$ —) had received from the eosin-bearing chromosome a normal piece to replace the damaged piece containing the region formerly occupied by bar and the vital allelomorphs.

STOCK OF DEFICIENCY

The possession of one deficient X (—) does not kill the female, which is saved by the action of the dominant vital allelomorphs carried by the other X. Half of the daughters of such a female receive this deficient X and repeat the genetic results of their mother. A stock of deficiency was kept by selecting in each generation the daughters containing the deficient X, and, as is the practice with all lethals, this selection was rendered certain by linkage.

THE INCLUSION OF FORKED IN THE DEFICIENT REGION

It now seemed probable that the X chromosome of that particular sperm which gave rise to the exceptional daughter must have lost⁴ a fragment containing the bar gene and also one or more genes necessary to the life of the animal. If this were the true explanation the chromosome should be deficient for all the genes within a definite distance of bar. It was anticipated that the section might be long enough to include more known loci than bar and the vital allelomorphs, and accordingly systematic tests were carried out with the mutations whose genes lie in the neighborhood of bar. The male, having but one X chromosome, is normally haploid with respect to all sex-linked genes; those females which have one normal X and one X deficient in the locus for a particular gene should behave with respect to that gene as if haploid and not as if diploid. That is, any recessive character whose locus lies opposite the deficient region should show itself in such a heterozygous female in spite of the fact that the character is normally a strict recessive, for in the deficient region there should be no active allelomorph to dominate.

Accordingly the next step was to test females carrying the deficient X, by forked, by rudimentary, and by fused, these being the recessive mutants with loci closest to bar (see map p. 457). The expected result was obtained with forked. Females heterozygous for deficiency, when outcrossed to forked males, gave half of their daughters forked, though these daughters were only heterozygous for forked! These forked daughters were derived from that half of the eggs which retained the deficient X, as was proved by the lethal result, as well as by the linkage relations shown by these forked females when they were bred (tables 4-8). This evidence shows that the mutation which removed the gene for bar and the vital allelomorphs, involved not simply these genes but also the normal genes of a section of the chromosome extensive enough to include the locus for forked.

THE MAXIMUM AND THE MINIMUM LENGTHS OF THE DEFICIENT REGION
AS MEASURED BY THE HAPLOID TESTS WITH THE RECESSIVES

In the case of the other recessives (rudimentary and fused) the result obtained with forked did not occur (tables 4 and 5, appendix), which shows that the maximum length of the deficient region is the interval be-

⁴ Since the results expected from complete inactivation are practically indistinguishable from those due to physical loss, consideration of the inactivation alternative will be deferred to a special section.

TABLE 3

The inclusion of forked in the deficient region as shown by tests of deficient-bearing females (\overline{w}) by forked males.

Culture	Daughters		Sons \overline{w}			
			\overline{w}		\overline{w}	
No.	<i>f</i> !	+	Dies	+	<i>w</i>	Dies
668	49	55	—	24	28	—
669	79	72	—	41	25	—
691	129	107	—	76	46	—
692	128	114	—	66	47	—
Total	385	348	—	207	146	—

tween and exclusive of these two recessives, which are the nearest unaffected characters on either side. This maximum length is about 4.4 units. These same tests together with the data from the origin of deficiency show that the minimum length is the interval between and including forked and bar (about half a unit). The test with fused, which lies nearer the end of the chromosome than forked and bar (see map p. 457), brought out another significant point, namely, that the deficient X had not lost the entire end of the chromosome, but rather was deficient for a section near the end, leaving the genetic materials unchanged beyond this region. By crossing over between the deficient region and fused, females have been obtained in which the deficient X carries fused in the normal piece beyond the deficient region (table 6, appendix).

THE ABSENCE OF CROSSING OVER WITHIN THE DEFICIENT REGION

It seemed probable that the lethal effect of deficiency was not simply due to the deficiency for forked and bar, but rather that the deficiency had affected all the loci between forked and bar, including one or more whose normal action was essential to the life of the fly. In general it is to be anticipated that cases of deficiency should act as lethals, since it seems probable that any very extensive piece includes a locus vital to the animal. Very small deficiencies might conceivably fail to include such a vital locus, and it was thought that such smaller sections of the forked-bar deficiency might be obtained by crossing over in a female carrying forked—bar deficiency in one X and forked and bar in the other X. ($\overline{f} \overline{B'} \rightarrow \overline{f} \overline{B'}$) In an effort to test this possibility 1716 males were raised, but these did not show any crossovers (table 14, ap-

pendix). Either all crossover males died because of having a lethal fragment of the deficient region, or there were no crossovers to live or die. In testing this question an experiment (table 9, appendix) was devised so that the crossovers among the females could be detected, there being no question that the crossover females would live. There were raised 3138 such females and not one of them was a crossover! In this number of females 16 were expected to be crossovers. It is evident that crossing over in the deficient region is abnormally low, if indeed there is any crossing over whatever in this region. This disappearance of crossing over from the deficient region is practically proof that the entire region was involved, a section between and including forked and bar and certain vital genes.

THE EXTENT OF THE DEFICIENT REGION MEASURED BY LINKAGE

It was found that crossing over in other parts of the deficient X was of approximately normal frequency (table 14, appendix), and this fact made it possible to find out more nearly the maximum length of the deficient region. The elimination of genes and of crossing over from the deficient region results in a shortening of the genetic chromosome by an amount equal to the length of the deficient region. How much closer together have rudimentary and fused been brought by the occurrence of deficiency? Normally there is 4.4 percent of crossing over between rudimentary and fused. When deficiency was present there was a drop of 0.7 unit in this value (table 10, ♀♀, and table 14). This drop of 0.7 unit is in agreement with the previous data which showed that the minimum length of the deficient region is 0.5 unit. Evidently, however, the deficient region does not extend much beyond the forked—bar section.

THE DOMINANCE RELATIONS OF BAR AND THE NATURE OF THE BAR-DEFICIENT MUTATION

The mutative process, of which the first detected effect was (1) the loss of the dominant bar gene, involved also (2) the loss of the normal allelomorph of the recessive mutation forked, whose locus is about half a unit distant from that of bar, and (3) the loss of certain vital allelomorphs, which, from the linkage relations probably occupied the section between forked and bar; and (4) the disappearance of crossing over from this same region, due presumably to the loss of the physical framework of the chromosome. All of these four distinct but correlated effects can therefore be met and explained by the single hypothesis of the physi-

cal loss of a definite section of chromosome which has been measured by two genetic methods. It seems unreasonable that one of these effects should be due to a cause different from that of the others but initiated at the same time, as, for example, that the apparent loss of the bar gene (B') should have been in reality due to a remutation to its original wild-type allelomorph (b'), a process which will in nowise account for the other observed changes which had their origin in the same region at the same time.

It will be recalled that the eye shape of the normal heterozygous bar female ($\text{—————}\frac{B'}{b'}$) is an intermediate between the narrow bar of the homozygote and the round eye of the wild female. It was found (table 7, appendix) that the female carrying bar in one X and bar-deficiency in the other ($\text{—————}\frac{\text{---}}{B'}$) was in somatic appearance like the normal bar heterozygote and not like the homozygous bar female. The fact that the bar male with its one X chromosome carrying a single bar gene has an eye practically as narrow as that of the homozygous bar female, shows that one bar gene is sufficient to produce a fully narrow eye. That the bar gene of the $\text{—————}\frac{\text{---}}{B'}$ female does not make her eye fully narrow must be due to some opposing action tending to broaden the eye. Since the other X is deficient for the bar locus this broadening action must be due to genes outside of the bar locus. In the broad-eyed $\text{—————}\frac{\text{---}}{B'}$ female there are two sets of such broadening genes but only one narrowing gene (B'), while in the narrow-eyed homozygous bar female there are two narrowing genes. The narrowness of the eye of the bar male can be ascribed to its having the same ratio of narrowing action (1 B' gene: 1 set of broadening genes) as has the narrow-eyed homozygous female (2 B' genes: 2 sets of broadening genes). Likewise the broadness of the normal heterozygous bar female is not due to the action of the b' gene, as formerly supposed, but is due to the half ratio of narrowing to broadening genes (1 B' gene: 2 sets of broadening genes).

The suggestion that the broad-eyed $\text{—————}\frac{\text{---}}{B'}$ females owed their broadness to being in reality $\text{—————}\frac{-b'}{B'}$ females, due to the occurrence of a crossover ($\text{—————}\frac{\text{---}}{b'} \rightarrow \text{—————}\frac{-b'}{B'}$) somewhere in the ancestry, is met by the evidence that in the ancestry opportunity to become such a crossover had been open to but a single female, and that she should be

such a crossover is incredible in view of the fact that in an experiment to test the amount of crossing over in the deficient region not one female in a total of over three thousand had proved to be a crossover.

The mutation responsible for deficiency may not have been, as so far assumed, the physical loss of a section of the chromosome; it may have been some kind of "inactivation," such as an internal rearrangement with change of properties, the loss of essential materials, or the addition of inhibiting agents. If inactivation is the explanation of deficiency then it must be complete inactivation; for in every case in which characteristics have disappeared, they have disappeared entirely. Thus, for example, the dominant bar gene retains no trace of its narrowing effect: the eye of a heterozygous female ($\text{———}\overline{\text{b}}'$) is wholly round, and the eye of the $\text{———}\overline{\text{R}}'$ female is no narrower than that of the regular heterozy-

gote. In favor of the inactivation view may be cited the striking analogy with the Y chromosome: the Y, while cytologically of the same nature as other chromosomes, is genetically of little significance, as is proved by the fact that the effect of sex-linked genes in the male is in no case altered by anything in the Y, by the fact that the supernumerary Y's obtained through non-disjunction are without effect upon the visible characters, and by the lethal effect,—a fly having one or two Y's but no X being unable to live. Furthermore, there is no crossing over between Y and X even when the Y is in a female (XXY) in which there is certainly synapsis between Y and X and in which the occurrence of crossing over between the other chromosomes shows that the failure of crossing over in the case of the Y is due to a peculiarity of the Y itself. Since the Y offers a case of a chromosome inactive with respect to both the genetic materials and the framework, it becomes possible to suppose that the case of deficiency is an example of the same process that has produced the inactivation of the Y. That a piece of the Y chromosome has actually been substituted for the corresponding piece of the X seems impossible because such a substitution would involve three very improbable occurrences, viz., (1) crossing over in the male, (2) crossing over of the Y chromosome, and (3) a double crossover embracing a section only about a half unit long, while the shortest section in which a double crossover is known to have occurred is 13.5 units long.

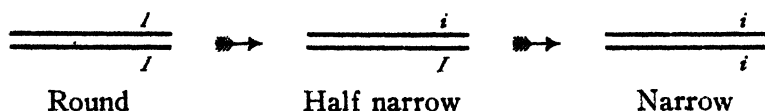
On the other hand, the "loss" view offers a more comprehensible solution for the fact that character genes different in nature but adjacent in position were affected by the one mutative change, and also for the fact that this one mutation affected, at the same time, the crossing over,

which seems to depend upon the framework of the chromosome rather than upon the character genes. As evidence that pieces may be lost bodily from chromosomes and that fragments may join together, there may be offered two distinct cases of "duplication" (unpublished), a phenomenon, the explanation of which seems to be that a section taken from the mid-region of one X has become attached to the end of the other X, its mate. The mid-region of the latter chromosome is represented twice, once in the normal location and again at the end. It seems probable that the first X, from which the duplicating fragment was taken bodily, would show the characteristics of deficiency, though in the two cases of duplication there was no evidence as to the fate of these terminal sections.

It seemed that a cytological examination might definitely settle this question, for on the loss view of deficiency the chromosome should be visibly shorter by an amount corresponding to the section lost. If the lost section were long enough, a difference in length between the two X's of a female having one deficient X should be observable. As stated in the beginning, the stock of deficiency was lost before the examination could be made. Several new cases which are possibly deficiencies in various parts of the X and even in other chromosomes have arisen, and it is hoped that combined cytological and genetic studies of these cases will make the subject clearer.

DEFICIENCY AND THE "PRESENCE AND ABSENCE" HYPOTHESIS

By following up the clue that a certain observed change might be due to the loss of a section of chromosome, we have been able to demonstrate a number of new and unusual facts which were predictable on that basis, and have thereby made it highly probable that the correct explanation has been found. This case of deficiency therefore constitutes the first valid evidence upon the question of "presence and absence." And it is significant to notice that the occurrence of the deficiency of a considerable section of genes has not brought to light any visible mutative changes in the way of dominants, contrary to what might well be expected on the presence and absence hypothesis. This is the more significant when it is recalled that the deficient region included the locus for bar,—a known dominant mutation. According to the presence and absence hypothesis the original appearance of the dominant bar character was due to the loss from the chromosome of an inhibitor, thereby allowing the normal narrowing effect of the remaining complex to assert itself.



Now, it should make no difference whether this inhibitor were lost by a special loss involving only the inhibitor or whether it were lost because of being situated in a particular section which itself became lost. In other words, the chromosome which is deficient for the region carrying the inhibitor should allow the occurrence of the same narrowing effect that is allowed by the simple loss of the inhibitor. In point of fact, the deficiency of the region in which the inhibitor must be hypothecated does not produce an effect like that of the mutation responsible for bar. For, the female carrying one deficient X and one normal X shows no narrowing of the eye shape, and likewise the female carrying one deficient X and one bar X is no narrower in eye shape than a normal heterozygous bar. Thus, in the only case which has a direct bearing on the presence and absence hypothesis, it is seen that the expedient of the loss of inhibitors to explain the origin of a dominant mutation is of no avail.

If, however, the appearance of the bar character were due to the creation of a new presence, then of course the loss of this presence by deficiency should restore the original condition; but that advocates of "presence and absence" have little liking for this type of explanation of the origin of a dominant is evident from the lengths they go in some recent expositions to avoid the vexed question of the origin of presences.

DEFICIENCY AND SEX DIFFERENTIATION

With non-disjunction the proof was complete that two X chromosomes determine a female and one a male. However, it has been suspected that the determiner of sex is not the "X-as-a-whole," but that in some definite part or parts of the X there are specific sex-differentiators. The case of deficiency favors this view; for, an XX individual having one deficient X is a *female*, normal in appearance and function. Two intact X's are not necessary for the production of a female; that is, sex-production is a function of some particular part of the X rather than of the X as a whole. Sex-differentiation was not affected by the occurrence of deficiency because the differentiators are in some region of the X other than the section from forked to bar.

THE REALITY OF THE CHROMOSOME MAPS

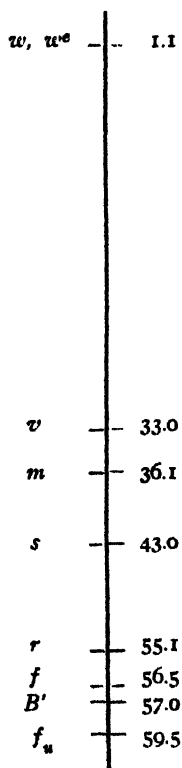
From the evidence of non-disjunction we know that the genes for the sex-linked characters are parts of the X chromosome. By means of

linkage studies we have been able to construct maps of the location of these sex-linked genes in a linear order which we believe to correspond to the linear structure of the chromosome. It has been objected that these maps may be only expressions of some "force" and that they do not correspond to an actual localization of genes along the chromosome. Deficiency furnishes the first direct evidence that the maps do correspond to a real localization of genes along the chromosome. That a single disturbing cause—the deficiency mutation—should exert a selective effect upon a certain few genes—bar, forked, vital allelomorphs—while leaving numerous other genes unaffected must be due to the possession by the few of a similarity either of properties or of location unshared by other genes. Nothing of the known properties of the dominant bar eye shape, the recessive forked bristle modification, and of the vital allelomorphs, are unique or suggest marked similarity to each other or dissimilarity between them and other sex-linked genes. *With regard to the location, however, there is independent and conclusive evidence from the linkage that these genes constitute a definitely localized and measurable section of the X chromosome.* The deficiency mutation was discovered because of its effect upon a single gene, viz., bar. It was then found to have affected at the same time one or more vital allelomorphs. When these vital allelomorphs are mapped according to the linkage shown, they are seen to occupy the region adjacent to bar. The argument from the location of forked within the deficient region is still stronger, for this location was detected and proved as the result of a deliberate search among those genes which had *previously been mapped closest to bar!* Nor does the evidence stop here, for not only did the deficiency mutation affect a section of adjacent genes but it also removed the crossing over from a definite section of chromosome. Now when the section from which the crossing over has been removed is compared upon the map with the section in which the genes are affected the two are seen to be identical. For a definite section of genes an identity has been established between the map and an actual distribution of genes.

APPENDIX

The sex-linked mutants referred to in this paper are: white eye color (w); eosin eye color (w^e), allelomorphic to white, and giving in females carrying white in one X and eosin in the other ($\frac{w}{w^e}$), an intermediate eye color, "white-eosin compound"; vermilion eye color (v); miniature wings (m); sable body color (s); rudimentary wings (r);

forked bristles (f); bar eye shape (B'); fused venation (f_u); and deficiency for the region between and including forked and bar (—). Flies which show no mutant characters are said to be wild-type (+). The symbols included in parentheses do double duty, both to represent the genes for the mutants, and to tell the somatic appearance of flies (table headings, etc.); the small letters represent recessive mutants, and the primed capitals dominant mutants. The localization of these genes along the X chromosome as calculated from the linkage relations is given by the accompanying map⁵ in which one unit of distance is one percent of total crossing over.



The two X chromosomes of the female are represented by two parallel lines with symbols showing the relative positions of the mutant genes involved ($\begin{smallmatrix} w \\ \hline v \end{smallmatrix}$), or more often by a single line, in which case the space above the line with its symbols represents one X and the space below, the other X ($\begin{smallmatrix} w \\ \hline v \end{smallmatrix}$). The chromosome which has the mutant gene farthest to the left of those involved in the cross is arbitrarily

⁵ From MORGAN and BRIDGES 1916, Carnegie Institution of Washington publication 237.

represented in the top space. The symbol $\frac{w^e}{v} \mid \frac{w^e}{v}$ is a contraction of

$\frac{w^e}{v} \xrightarrow{\quad} \frac{w^e}{v} \xrightarrow{\quad} \frac{w^e}{v}$, and denotes that,

by crossing over in a female which carries eosin in one X and vermillion in the other, the two eggs, eosin vermillion and wild-type, are produced. The zygote arising from the egg represented by the upper space is always written in the column to the left in the double column beneath the crossover symbol; likewise the column to the right corresponds to the egg of the lower space. By following this convention, we may often omit from the tables the individual headings of the two included columns (e.g., see table 11). In place of the crossover symbol, it is often advantageous to use the "crossover formula" as in table 13.

Thus, in the first case in table 13, $(\frac{w^e}{vm} \mid \frac{f}{R'})$, the "o" represents the sum of the flies that came from the two non-crossover gametes, eosin forked and vermillion miniature bar; the "1" represents the single crossovers between eosin and vermillion, that is, in the "first crossing over region"; the "1, 3 double crossovers" represent the flies resulting from the gametes $\frac{w^e}{v} \mid \frac{vm}{f}$; etc.

TABLE 4

The non-inclusion of rudimentary in the deficient region as shown by the tests of deficient-bearing females by rudimentary males.

Forked females ($\frac{w^e}{f}$) from culture 857, table 9a.

No.	Daughters		Sons*			
	+	r	$\frac{w^e}{f}$	$\frac{w^e}{f}$	$\frac{w^e}{f}$	Dies
994	42	0	—	22	10	—
997	116	0	—	29	23	—
998	79	0	—	26	22	—
999	147	0	—	35	32	—
Total	384	0	—	112	87	—

* When females are heterozygous for deficiency and for forked, crossing over in the deficient region (if it occurs) should give the two contrary classes, non-forked sons and forked sons ($\frac{w^e}{f} \mid \frac{w^e}{f}$). These sons should live only if they escaped retaining a lethal fragment of the deficient origin. The observed total lack

of any non-forked sons among the offspring is then additional evidence that no cross-overs occur, or that these crossovers die. However, the forked crossovers would not be distinguished from the forked non-crossovers, and therefore this sort of evidence is equivalent only to a half amount as compared with the data of tables 6 and 8. Accordingly, in table 14, the data from males on crossing over in the deficient region includes all the males of tables 6 and 8, but only half the males of tables 4, 5, 7, 9, and 9 A.

TABLE 5

The non-inclusion of fused in the deficient region as shown by the tests of deficient-bearing females by fused males.

Forked females ($\frac{w^e}{f}$) from culture 857, table 9A.

No.	Daughters		Sons			
			$\frac{w^e}{f}$		$\frac{w^e}{f}$	
	+	f_w	Dies	f	w^ef	Dies
988	118	0	—	37	13	—
989	71	0	—	27	16	—
991	206	0	—	50	44	—
993	175	0	—	40	27	—
Total	570	0	—	154	100	—

TABLE 6

The insertion of fused into the intact region beyond the deficient region.

No.	♀ ♀	♂ ♂ *			
		$\frac{f}{f} B'$	f_w	$\frac{f}{f} B' f_w$	
		Dies	fB'	Dies	$fB'f_w$
1755	134	—	58	—	1
2176	30	—	11	—	1
Total	164	—	69	—	2

* These males are not included in the summary of table 14 as showing the amount of crossing over between deficiency and fused, for there might be other like cultures (table 8) which failed of detection because no crossover occurred. A crossover value calculated from such incomplete data could only be regarded as a maximum value.

TABLE 7

Tests of the relation between deficiency and bar by outcrossing deficient-bearing females (from culture 668, table 3) to bar males.

No.	♀ ♀	♂ ♂			
		$\frac{w^e}{f}$	$\frac{w^e}{f}$	$\frac{w^e}{f}$	$\frac{f}{f}$
	B'	Dies	f	w^ef	Dies
749	60	—	17	11	—
751	24	—	8	3	—
754	52	—	19	15	—
Total	136	—	44	29	—

TABLE 8

The non-occurrence of crossover sons of deficient-bearing mothers heterozygous for forked and bar ($\frac{f}{f} B'$).

No.	Daughters	Sons			
		$\frac{f}{f} B'$	$\frac{f}{f} B'$	$\frac{f}{f} B'$	$\frac{f}{f} B'$
		Dies	fB'	B'	f
1200	51	—	33	—	—
1313	81	—	35	—	—
1752	97	—	25	—	—
1753	79	—	43	—	—
1754	114	—	64	—	—
1756	54	—	38	—	—
1757	41	—	26	—	—
1981	130	—	57	—	—
1981r	39	—	21	—	—
2177	41	—	31	—	—
Total	727	—	373	—	—

TABLE 8A

Mothers heterozygous for sable also ($\frac{s}{-} \frac{f}{-} \frac{B'}{-}$).

		$\frac{s}{-} \frac{f}{-} \frac{B'}{-}$		$\frac{s}{-} \frac{f}{-} \frac{B'}{-}$		$\frac{s}{-} \frac{f}{-} \frac{B'}{-}$	
		sfB'	Dies	Dies	fB'	sf	B'
1145	124	50	—	—	12	—	—
1758	78	17	—	—	3	—	—
1759	38	17	—	—	2	—	—
1764	107	35	—	—	10	—	—
1765	97	31	—	—	4	—	—
1766	36	12	—	—	4	—	—
1767	113	49	—	—	11	—	—
Total	593	211	—	—	46	—	—

TABLE 9

The non-occurrence of crossover daughters when deficient-bearing mothers heterozygous for bar ($\frac{-}{-} \frac{-}{-} \frac{B'}{-}$) were backcrossed to forked males.

No.	Daughters				Sons			
	$\frac{-}{-} \frac{B'}{-}$		$\frac{-}{-} \frac{B'}{-}$		$\frac{-}{-} \frac{B'}{-}$		$\frac{-}{-} \frac{B'}{-}$	
	f	B'	fB'	+	Dies	B'	B'	+
2222	77	90	—	—	—	76	—	—
2223	69	66	—	—	—	49	—	—
2224	60	64	—	—	—	69	—	—
2234*	75	64	—	—	—	69	—	—
2235	77	81	—	—	—	61	—	—
2236	51	50	—	—	—	34	—	—
2238	51	71	—	—	—	71	—	—
2239	68	53	—	—	—	65	—	—
2240	82	61	—	—	—	49	—	—
2241	54	59	—	—	—	46	—	—
2246	77	70	—	—	—	58	—	—
2260	85	82	—	—	—	113	—	—
2261	42	32	—	—	—	11	—	—
2264	86	73	—	—	—	81	—	—
2265	62	90	—	—	—	76	—	—
2286	48	49	—	—	—	56	—	—
2290	93	127	—	—	—	111	—	—
2316	79	106	—	—	—	86	—	—
2320	37	70	—	—	—	77	—	—
Total	1273	1358	—	—	—	1258	—	—

TABLE 9 A

Mothers heterozygous for eosin also ($\frac{w^e}{B'}$).

					$\frac{w^e}{B'}$	$\frac{w^e}{B'}$	$\frac{w^e}{B'}$	$\frac{w^e}{B'}$
					Dies	Dies	Dies	+
857	60	83	—	—	48	24	—	—
858	108	121	—	—	48	47	—	—
859*	60	75	—	—	40	29	—	—
Total	228	279	—	—	136	100	—	—

* In each of the cultures 2234 and 859 a sterile forked male (XO) appeared, due to primary non-disjunction.

TABLE 10

The crossing over in deficient-bearing females heterozygous for rudimentary and fused ($\frac{r}{f_u}$).

No.	Daughters				Sons*							
	$\frac{r}{f_u}$		$\frac{r}{f_u}$		$\frac{r}{f_u}$		$\frac{r}{f_u}$		$\frac{r}{f_u}$		$\frac{r}{f_u}$	
	$r f_u$		r	f_u	$r f_u$	Dies	Dies	f_u	r	Dies		
1437	17	80	0	2	20	—	—	0	1	—		
1438	43	89	1	1	41	—	—	1	2	—		
1599	27	51	3	1	40	—	—	2	0	—		
1600	45	66	2	3	56	—	—	2	0	—		
1601	38	59	1	1	37	—	—	1	0	—		
1619	21	37	1	3	12	—	—	0	0	—		
1696	18	37	0	2	16	—	—	0	0	—		
1697	15	21	2	0	8	—	—	1	0	—		
1700	21	26	1	3	10	—	—	0	2	—		
Total	245	466	11	16								
1775		80			16	—	—	1	1	—		
1778		31			10	—	—	0	0	—		
1779		67			16	—	—	0	1	—		
1905		31			15	—	—	0	0	—		
1906		31			19	—	—	0	1	—		
2106		100			32	—	—	4	1	—		
2107		67			14	—	—	0	1	—		
2175		56			31	—	—	1	1	—		
Total		463			393	—	—	13	11	—		

* The males of table 10 are not included in the summary of table 14, because of the difficulty of calculating the true amount of crossing over when a lethal (deficiency) and a poorly viable mutant (rudimentary) are both present. Ordinarily the poor viability of a mutant has little effect upon the apparent amount of crossing over, because, in each pair of contrary classes, the relative smallness of the class in which the non-viable mutant occurs is counterbalanced by the relative largeness of the contrary class in which its viable normal allelomorph occurs. This is the case with the females

of table 10. But when a lethal also is present (as in the case of the males of table 10), the lethal kills one of each pair of contrary classes and hence certain classes are relatively too low (as, in table 10, the non-crossover class rudimentary fused and the "2" crossover class rudimentary), while certain other classes are relatively too high (as the "1" crossover class fused). That the males of table 10 are in agreement with the females is evident after a correction has been made for the disturbance due to the unbalanced non-viability. The females of table 10 gave the interval between rudimentary and fused as 3.7 units, instead of the normal 4.4, a decrease of .7 unit due to the deficient region. The percentage expectation for the males on this basis (the distance from rudimentary to the deficient region = 1.4, the length of the deficient region = .7 unit, and deficiency to fused = 2.3) is "o" = 96.3, "1" = 1.4, and "2" = 2.3. These percentages become "o" = 94.24, "1" = 3.11, and "2" = 2.65 if 44 percent of the rudimentary and 88 percent of the fused zygotes hatch. The observed percentages are "o" = 94.24, "1" = 3.12, and "2" = 2.64. The assumed percentages of viability of rudimentary and of fused are in agreement with the results of other experiments in which these mutants are involved.

TABLE 11
The linkage of white and deficiency.

No.	Daughters	w —		w —	
		—	—	—	—
632	166	—	34	14	—
642	123	—	40	35	—
645	264	—	82	53	—
647	216	—	59	35	—
731	58	—	32	12	—
Total	827	—	247	149	—

TABLE 12
The linkage of sable and deficiency.

s — females backcrossed to sable forked males.

No.	Daughters				Sons			
	s —		s —		s —		s —	
	s	f	sf	+	s	Dies	Dies	+
1024	34	39	5	8	31	—	—	5
1025	27	26	5	7	21	—	—	6
1026	34	39	6	9	33	—	—	6
1201*	41	52	8	11	49	—	—	3
1242	73	73	8	14	72	—	—	7
1244	29	20	5	3	27	—	—	6
Total	238	249	37	52				
867			111		58	—	—	11
900			81		35	—	—	5
975			88		44	—	—	10
1120			83		41	—	—	11
Total			363		411	—	—	70

* In culture 1201 a sterile sable forked male (XO) appeared, due to primary non-disjunction.

TABLE 13

Incidental linkage data not involving deficiency.

Genes	No.	Classes with respect to crossing over						
$\frac{we}{vm} \frac{f}{B'}$	862	0	1	2	3	1, 3	2, 3	1, 2, 3
		45	30	2	23	8	1	1
$\frac{we}{B'} \frac{f}{B'}$	861	0			1			
		42			22			
$\frac{vm}{f} \frac{B'}{B'}$	863	0		1		2		
		68		2		31		
$\frac{s}{f}$	864	0			1			
		102			27			
	865	123			22			
	866	92			18			
	868	80			9			
	869	137			15			
	870	139			25			
	871	75			15			
	872	131			19			
	873	77			9			
	885	44			7			
	1235	152			27			
	1243	267			39			
	Total		1419			232		
$\frac{r}{B'}$	2263	0			1			
		153			3			
$\frac{r}{B'} \frac{f_u}{f_u}$	2242	0		1		2		
		111		3		8		
	2243	66		1		2		
	2245	24		1		2		
	2262	15		1		0		
	2267	192		0		7		
	2287	114		3		5		
	2289	131		2		5		
	2291	132		1		3		
	2317	112		3		1		
	2318	157		4		5		
	2319	85		2		1		
	2352	94		1		3		
	Total		1233		22		42	
$\frac{r}{f_u}$	1174	0			1			
		49			0			
	1175	20			0			
	1207	110			3			
	1208	91			5			
	1209	101			3			
	1281	106			3			
	1282	47			1			
	1308	113			4			
	Total		637			19		

TABLE 13 (Continued)

Genes	No.	Classes with respect to crossing over	
		0	1
$\frac{f}{B'}$	860	379	1
	1021	163	3
	1022	163	1
	Total	705	5
B'		0	1
$\frac{B'}{f_u}$	2244	100	4

TABLE 14

A summary of the linkage data of this paper.

Genes	Total	Crossovers	Percent
$w \ v$	110	39	35.4
$w \ m$	110	41	37.3
$w \ —$	1562	625	40.0
$w \ f$	174	78	44.8
$w \ B'$	174	78	44.8
$v \ m$	211	6	2.8
$v \ f$	211	66	31.3
$v \ B'$	211	66	31.3
$m \ f$	211	64	30.3
$m \ B'$	211	64	30.3
$s \ —$	1314	205	15.6
$s \ f$	1651	232	14.0
$r \ B'$	1453	25	1.7
$r \ f_u$	1953	83	4.3
$r \ \frac{f_u}{—}$	738	27	3.7
$f \ B'$	980	5	0.5
$(\frac{f \ B'}{—})$	$\left\{ \begin{array}{l} \text{♂♂} \ 1716 \\ \text{♀♀} \ 3138 \end{array} \right.$	0	0.0
$B' \ f_u$	1401	0	0.0
		46	3.3

DOMINANCE OF LINKED FACTORS AS A MEANS OF ACCOUNTING FOR HETEROSIS¹

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A stimulation resulting from hybridization in both plants and animals has long been recognized. The increased growth as the result of crossing is so common an occurrence that it is probably familiar to everyone who has made any hybridization experiments.

This stimulation, variously spoken of as "hybrid vigor," stimulus due to heterozygosis, heterosis, etc., was clearly established as an organic phenomenon by the abundant cases cited by early investigators such as KÖLREUTER (1766), GÄRTNER (1849), DARWIN (1877) and FOCKE (1881), as well as a large number of other investigators at that time and an increasingly large number since then. The important investigations in recent times (EAST 1908, 1909; SHULL 1908, 1909, 1910, 1911; EAST and HAYES 1912) are so familiar that it is not necessary to do more than mention them.

Concrete explanations as to the cause of these results have not accompanied the accumulation of facts. Various hypotheses have attempted to account for the results, but they have been little more than outlines of the problem.

The valuable contributions of EAST (1908, 1909) and of SHULL (1908, 1909, 1910, 1911) established the fact that continued inbreeding is not a process of continuous degeneration but that the reduction in the amount of growth is due to the isolation of unlike biotypes differing in the amount of growth attained at normal maturity. Together with this isolation of biotypes there was a loss of a stimulation which was assumed to be derived in some way from crossing. This decrease of vigor becomes less after continued inbreeding and to all appearances ceases as complete homozygosis is approached. This stimulation has been shown to be correlated more or less closely with the degree of heterozygosity. The whole subject has been ably presented and discussed by EAST and

¹Contribution from the CONNECTICUT AGRICULTURAL EXPERIMENT STATION and from the Bussey Institution of HARVARD UNIVERSITY.

HAYES (1912). A quotation from this paper (pp. 36 and 37) presents the matter as it stands at present:

"The hypotheses in regard to the way by which the act of fertilization initiates development are numerous, but since they are entirely speculative it is not necessary to discuss them here. The only conclusion that seems justified is that they are not immediately psychological or vitalistic in nature. LOEB's remarkable researches prove this. But whatever may be the explanation of the means by which the process is carried out, the statement can be made unreservedly that the heterozygous condition carries with it the function of increasing this stimulus to development. It may be mechanical, chemical, or electrical. One can say that greater developmental energy is evolved when the mate to an allelomorphic pair is lacking than when both are present in the zygote. In other words, developmental stimulus is less when like genes are received from both parents. But it is clearly recognized that this is a statement and not an explanation. The explanation is awaited."

KEEBLE and PELLEW (1910) first suggested a concrete explanation to account for the results of this nature which they obtained with peas. Two varieties of garden peas, as grown by them, each averaged from 5 to 6 feet in height. The F_1 grown from this cross averaged from 7 to 8 feet in height, 2 feet taller than either parent. A result of this kind is comparable to heterosis. The F_2 was put into four classes: one class containing plants as tall as the F_1 , two classes of semi-tall plants similar in height to the two parents, and one class of dwarfs shorter than either parent. The two classes of semi-tall plants, similar in height, were differentiated in the same manner as the two parents; one had thick stems and short internodes, the other had thin stems and long internodes. Other differences helped to distinguish the two classes of equal height. The number of plants falling into these four classes agreed closely with the expectation from a di-hybrid ratio where two factors showing dominance were concerned, giving a 9:3:3:1 ratio.

The writers assumed two factors to be concerned: one producing thick stems, the other long internodes. These factors they designated *T* and *L*. One of the parental varieties was medium in height because it possessed one of these factors, e.g., that for thick stems, but lacked the other. Such a plant had the formula *TTll*. The other variety was of medium height because it lacked this *T* factor but possessed the factor for long internodes, and was given the formula *ttLL*. Both of these factors showed dominance over the allelomorphic condition; hence the F_1 was taller than either parent because both factors were present together. Whether or not later investigations have justified the interpretation that KEEBLE and PELLEW have placed on the data as explaining height of

their peas makes no material difference to the discussion here. Taken as it stands, it is a beautiful illustration of the way in which dominance may increase a character in F_1 over the condition of either parent.

Curiously enough, this explanation has never been considered an adequate one or in any way essentially related to the universal phenomenon of heterosis. This hypothesis of dominance accounting for heterosis, as outlined by KEEBLE and PELLEW, has two objections which have up to the present been considered insurmountable.

The chief objection has been that, if heterosis were due to the dominance of a greater or less number of factors governing the amount of development, it would be possible in generations subsequent to the F_2 to recombine in one homozygous race all of the factors resulting in large growth and, conversely, the negative condition in another homozygous race. In other words, it would be possible to obtain one strain having all of the dominant factors, and another with all of these dominant factors lacking. Both of these races should be homozygous, hence self-fertilization should not result in less vigorous progeny. The completely recessive race should be below the parents in its power for development, as the F_1 and the complete dominant were above the parents. That all of these supposedly necessary corollaries are not supported by the facts is well known.

Both SHULL (1911) and EAST and HAYES (1912) have considered this objection to be valid. A quotation (p. 39) from the latter makes their position on this point clear.

"KEEBLE and PELLEW (1910) have recently suggested that 'the greater height and vigor which the F_1 generation of hybrids commonly exhibit may be due to the meeting in the zygote of dominant growth factors of more than one allelomorph pair, one (or more) provided by the gametes of one parent, the other (or others) by the gametes of the other parent.' We do not believe this theory is correct. The 'tallness' and 'dwarfness' in peas which KEEBLE was investigating is a phenomenon apparently quite different from the ordinary transmissible size differences among plant varieties. Dwarf varieties exist among many cultivated plants, and in many known cases dwarfness is recessive to tallness. It acts as a monohybrid or possibly a dihybrid in inheritance, and tallness is fully dominant. Varietal size differences generally show no dominance, however, and are caused by several factors. Transmissible size differences are undoubtedly caused by certain genetic combinations (EAST 1911), but this has nothing to do with the increase of vigor which we are discussing. The latter is too universal a phenomenon among crosses to have any such explanation. Furthermore, such interpretation would not fitly explain the fact that all maize varieties lose vigor when inbred."

Another objection to the hypothesis of dominance has been raised by

EMERSON and EAST (1913). In this publication it is said that, if the effect of heterosis were due to dominance, the distribution of the F_2 individuals would be unsymmetrical in respect to characters in which heterosis was shown in F_1 . This follows from the familiar Mendelian expectations where there is dominance and any number of factors is concerned. For the purpose of illustrating this point let us take the case of height of peas already cited. In the F_2 population a distribution of the individuals in respect to height is, theoretically, 9 tall plants (with both factors present), 6 medium-tall plants (3 with one factor + 3 with the other), and one short plant (with both factors lacking).

Similar asymmetrical distributions in F_2 would occur with any number of factors (if there were no other facts to be taken into consideration), as seen from the figures given in table 1 modified somewhat from those given by BAUR (1911, p. 63).

In any case of a size character similar to height of peas with any number of factors, the plotting of the number of individuals in F_2 occurring in the classes given in row B in table 1 would give an asymmetrical distribution. This is on the assumption that the individual having the greatest number of dominant factors present (whether in the simplex or duplex state) would attain the greatest development of the size character.

In the vast amount of data accumulated upon the inheritance of quantitative characters no such tendencies toward an asymmetrical distribution is evident in the majority of cases recorded. In EMERSON and EAST's paper, referred to, dealing with quantitative characters in maize, and in HAYES's publication (1912) dealing with the same type of characters in tobacco, the distributions in F_2 , where heterosis is shown in F_1 , are all considered to be of the type of normal frequency distributions. If any skewness is shown by any of these it is too slight to suggest the types of curves obtained by plotting the figures in table 1, B.

It is perfectly evident that the two objections raised against the hypothesis of dominance as a means of accounting for heterosis, as outlined by KEEBLE and PELLEW, and as it has been considered up to the present, are valid. But both these objections to dominance as an interpretation of heterosis have failed to take into consideration the fact of linkage.

Abundant evidence is fast being accumulated² to show that characters are inherited in groups. The different theories accounting for this link-

² It is unnecessary to give references to the convincing results obtained by MORGAN, BATESON, and their collaborators, as well as to those obtained by many others whose work is of great importance if not so extensive.

TABLE I

Distribution of F_2 individuals when each character shows complete dominance and each has a visible effect.

Number of factors in which the F_1 is heterozygous	Distribution of the individuals		Total number in the population
1	A	3:1	4
	B	3:1	
	C	1:0	
	D	1:1	
2	A	9:3:3:1	16
	B	9:6:1	
	C	2:1:0	
	D	1:2:1	
3	A	27:9:9:9:3:3:3:1	64
	B	27:27:9:1	
	C	3:2:1:0	
	D	1:3:3:1	
4	A	81:27:27:27:27:9:9:9:9:3:3:3:1	256
	B	81:108:54:12:1	
	C	4:3:2:1:0	
	D	1:4:6:4:1	
n	A	$3^n : 3^{n-1} : 3^{n-1} : 3^{n-1} : 3^{n-1} : 3^{n-2} : 3^{n-2} : \text{etc.} \dots : 1$	$(2^n)^2$
	B	$1(3^n) : D(3^{n-1}) : D(3^{n-2}) : \dots \text{etc.} \dots : 1$	
	C	$n : n-1 : n-2 : \dots \text{etc.} \dots n-n$	
	D	$1 : \dots \text{etc.} = \text{coefficients of the expanded binomial } (a+a)^n \dots : 1$	

A, The distribution into the visibly different categories. B, The distribution into categories with different numbers of dominant factors present (either in a homozygous or heterozygous condition). C, The number of dominant factors in which the categories differ. D, The number of visibly different categories with the same number of dominant factors present.

age of characters make no essential difference in the use to which these facts will be put here. It is only necessary to accept as an established fact that characters are inherited in groups and that it is these groups of factors which Mendelize. The chromosome view of heredity, as developed by MORGAN and others (1915), will be used because it gives a means of representation in a simple, graphical manner.

The increasing complexity of Mendelism points very strongly to the probability that the important characters of an organism are determined by factors represented in all or most of the chromosomes or linkage groups. This idea has been proposed by EAST (1915) and seems to be in accord with the facts. If this view is approximately correct, and if it

may also be assumed that, in addition to the factors which differentiate varieties, many different factors may bring about the same visible effect, then it is possible to meet the two objections raised against dominance as a means of accounting for heterosis.

As an illustration of what is meant by different factors bringing about the same visible effect, an example may be taken in which one variety of plants grows to an average height of six feet because of one set of factors, and another variety grows to approximately the same average height but attains this height through the operation of a different set of factors. This is comprehensible when it is remembered that height is only an expression of a plant's power to develop. Hereditary factors which affect any part of the plant may indirectly determine height. Direct proof as to the essential correctness of this assumption, i.e., of different factors producing the same somatic effect, is at hand in the cases of duplicate genes producing the same morphological result in *Avena sativa* (NILSSON-EHLE 1909) and *Bursa bursa-pastoris* (SHULL 1914), as well as the other cases of duplicate genes reported by NILSSON-EHLE (1908) and EAST (1910).

The widespread occurrence of abnormalities and other characters detrimental to the organism's best development is well known in both the plant and animal kingdoms. This is especially true in naturally cross-pollinated species of plants. It may be taken for granted that no one variety has all of these unfavorable characters nor, on the other hand, has it all the favorable characters. For the most part each variety possesses a random sample of the favorable and unfavorable characters. There are differences between varieties in their power for development, however, just as there are differences in superficial characters. Some varieties of plants grow taller than others; some grow faster; some produce more seed. But, on the average, most of the varieties of a species tend to grow to about the same extent, however much they may differ in superficial characters.

If, for the most part, these favorable characters are dominant over the unfavorable (if normalities are dominant over abnormalities) it is not necessary to assume complete dominance in order to have a reasonable explanation of the increased development in F_1 over the average of the parents or any subsequent generation. It is in F_1 , and in F_1 only, that the maximum number of different factors can be accumulated in any one individual.

Because of linkage it is impossible to recombine in any one individual in later generations any greater number of characters in the homozygous

condition than were present in the parents if the factors were distributed uniformly in all of the chromosome pairs. Possible exceptions to this statement will be discussed later. This view of the situation explains why the effects of heterozygosis result in a greater development in F_1 than in the parents, and not less. Why should crossing not have resulted in a depressing or indifferent effect instead of a stimulating one, according to previous views?³ It also makes it seem probable that the effects of heterozygosis remain throughout the life of the sporophyte, even through innumerable asexual generations. Furthermore, it will be shown that no skewness in the distribution of F_2 is expected.

Let me submit in the form of a concrete illustration the abstract view that I have tried to present in the preceding paragraphs. A purely hypothetical case will be assumed, in which two homozygous varieties of plants, having three pairs of chromosomes, both attain approximately the same development as represented by any measurable character. This development will be considered to amount to 6 units, 2 of which are contributed by each chromosome pair. One of these varieties, which will be called "X," attains this development because of factors distributed in the three pairs of chromosomes. Any number of factors may be chosen, but, for the sake of simplicity, only three in each chromosome will be employed. These are numbered 1, 3, 5; 7, 9, 11; and 13, 15, 17; in the following diagram, each different in its contribution to the plant's development. The other variety, "Y", develops to an equal extent in the character measured, and this development will also be considered to amount to 6 units. It attains this same development, however, by a different set of factors distributed in the three chromosomes, numbered 2, 4, 6; 8, 10, 12; and 14, 16, 18. It is also assumed that these 6 factors are fully as effective in the $1n$ condition as in the $2n$ condition,*i.e., show perfect dominance. It will be seen from the diagram that the F_1 develops to twice the extent of either parent, because there are present here 18 different factors (in the $1n$ condition), whereas the parents have only 9 (in the $2n$ condition). In the diagram, any other factorial complex common to both varieties is ignored. The development of the parents of 6 units and of the F_1 of 12 units is additional to that afforded by this common factorial complex.

Following this hypothetical case into the F_2 generation by selfing or

³ Crosses between plants not closely related do result in no greater development than the parents and in many cases much less than the parents. This is because characters which are widely dissimilar are unfavorable to the organism's best development when acting together.

breeding together these F_1 plants, the theoretical results given in table 2 are obtained.

Summing up the results of this tabulation, it will be found that eight plants are homozygous and have the same development as either parent, i.e., of six units. Eight plants are heterozygous in all three chromosome

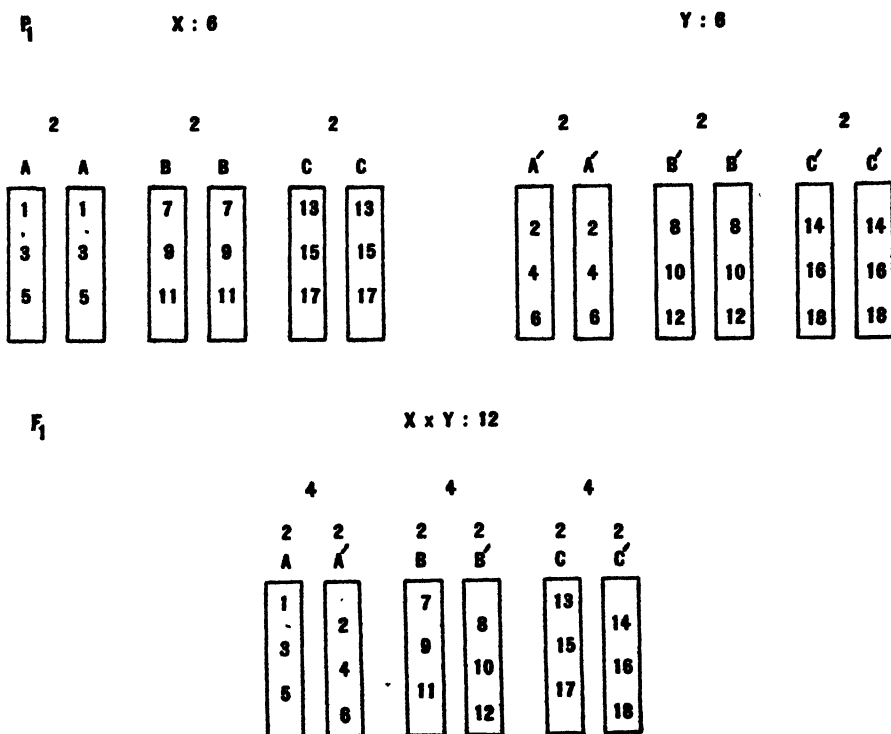


DIAGRAM 1.—To show how factors contributed by each parent may enable the first generation of a cross to obtain a greater development than either parent.

pairs and have the same amount of growth as F_1 , i.e., of twelve units. The remaining 48 plants fall into two equal-sized groups developing to eight and ten units respectively. In other words, the distribution is symmetrical, and this symmetry remains, however many chromosomes are concerned.

Furthermore, it should be noted that the mean development of F_2 is nine units, which is an excess above the parents of just half of the excess of the F_1 over the parents. In other words, the extra growth derived by crossing the two varieties has diminished 50 percent. In F_3 , from a random sample of F_2 , it can be shown that this excess again diminishes 50 percent, so that the effect is only 25 percent as great in F_3 as in F_1 ,

TABLE 2

Composition of a tri-hybrid in F_2 according to Mendelism, and the development which each individual attains depending upon the number of heterozygous chromosomes contained and thereby the total number of different factors present.

Number of individuals in each category	Categories	Contribution of each chromosome pair	Total development
1	A A B B C C	2 + 2 + 2	6
2	A A' B B C C	4 + 2 + 2	8
2	A A B B' C C	2 + 4 + 2	8
2	A A B B C C'	2 + 2 + 4	8
4	A A' B B' C C	4 + 4 + 2	10
4	A A B B' C C'	2 + 4 + 4	10
4	A A' B B C C'	4 + 2 + 4	10
8	A A' B B' C C'	4 + 4 + 4	12
1	A A B B C' C'	2 + 2 + 2	6
2	A A B B' C' C'	2 + 4 + 2	8
2	A A' B B C' C'	4 + 2 + 2	8
4	A A' B B' C' C'	4 + 4 + 2	10
1	A A B' B' C C	2 + 2 + 2	6
2	A A B' B' C C'	2 + 2 + 4	8
2	A A' B' B' C C	4 + 2 + 2	8
4	A A' B' B' C C'	4 + 2 + 4	10
1	A' A' B B C C	2 + 2 + 2	6
2	A' A' B B' C C	2 + 4 + 2	8
2	A' A' B B C C'	2 + 2 + 4	8
4	A' A' B B' C C'	2 + 4 + 4	10
1	A' A' B' B' C C	2 + 2 + 2	6
2	A' A' B' B' C C'	2 + 2 + 4	8
1	A' A' B B C' C'	2 + 2 + 2	6
2	A' A' B B' C' C'	2 + 4 + 2	8
1	A A B' B' C' C'	2 + 2 + 2	6
2	A A' B' B' C' C'	4 + 2 + 2	8
1	A' A' B' B' C' C'	2 + 2 + 2	6
64 Total			

Distribution of the F_2 individuals according to the development attained.

Classes	6	8	10	12	= 4	Number of classes
Frequency	8	24	24	8	= 64	Total population

and so on in subsequent generations. This is in accord with the mathematical prediction made by EAST and HAYES (1912), to which actual data obtained from maize roughly approximate, as shown by JONES (1916).

The development attained by any individual in table 2 is correlated with the number of heterozygous factors present. This has been main-

tained by all recent writers on the subject as a rough description of the facts as obtained in actual experiments.

When different numbers of chromosomes are concerned, according to this scheme, the number of individuals in the different classes making up the whole F_2 population is given in table 3.

In any F_2 distribution there are as many individuals heterozygous for all factors (duplicating F_1 individuals) as there are individuals homozygous for all factors concerned in the original cross (two duplicating the parents; the remaining forming new homozygous combinations). The remaining individuals fall into a symmetrical distribution between these two end classes. The theoretical figures for any F_2 distribution in which n Mendelizing units are concerned can be obtained by taking the coeffi-

TABLE 3

Distribution of the individuals in F_2 according to the number of heterozygous chromosomes pairs they contain.

Number of chromosome pairs in which the F_1 is heterozygous	Classes with different number of heterozygous chromosome pairs and the number and ratio of individuals in these classes						Total number of individuals in the population
	0	1	2	3	4	5	
1	1	1					4
2	4	8	4				16
3	16	64	96	64	16		256
4	32	160	320	320	160	32	1024
5	1	5	10	10	5	1	
n	2^n etc.	$2^n \times (\text{coefficients})$ etc.	2^n		$(2^n)^2$
	1 etc.	coefficients of the expanded binomial $(a + a)^n$ etc.	1		

cients of the expanded binomial $(a + a)^n$ and multiplying these by 2^n , as shown in table 3. Since the expanded binomial is used to illustrate a normal frequency distribution, there can be no question as to the symmetry of the F_2 distributions if the diagrammatic scheme outlined is, in this respect, a description of the actual facts.

In the preceding purely diagrammatic representation of the way in

which dominance may account for the effects of heterozygosis, perfect dominance was assumed. Such an assumption is neither justified nor desirable. Many theoretical explanations of the inheritance of quantitative characters are based on exactly the converse assumption, i.e., that factors in the *1n* condition have just half the effect that they have in the *2n* condition.

In the development of an organism, however, all types of factors are concerned, both qualitative and quantitative. Partial dominance in qualitative characters is a normal occurrence. The consensus of opinion at the present time is that there may be, in reality, no cases of perfect dominance. In those cases in which the heterozygote cannot be distinguished from the pure dominant, it is assumed that the similarity is only apparent and not real. The heterozygote merely approaches the condition of the dominant type more or less closely. However much it may be true that perfect dominance rarely or never occurs, the fact and universality of partial dominance can hardly be denied.

In this connection it should be realized that the difference between the heterozygote and the recessive type in many cases is one of *kind*, while the difference between the heterozygote and the dominant type is one of *degree*. A good illustration of this point is found in the case of albinism in maize. Plants heterozygous for the factor (or factors) determining the production of chlorophyll cannot be distinguished from normal green plants—a case of apparently complete dominance. If there is in reality a difference between these heterozygous and homozygous normal green plants, although not apparent, that difference is very slight as compared with the difference between the heterozygote and the abnormal recessive. In the former case the difference, if there is any, is quantitative. The heterozygote may not have as much chlorophyll as the normal homozygote. In the second case the difference is qualitative. The heterozygote has chlorophyll; the recessive has none. This is a difference which determines the life or death of the organism.

All the evidence at hand leads to a seemingly logical conclusion, one necessary to the conception of dominance as an explanation of heterosis, which is, that *many factors in the 1n condition have more than one-half the effect that they have in the 2n condition*. Whether or not this is a logical conclusion and one that is justified by the facts remains to be seen. It certainly has the advantage of being more definite and comprehensible than the assumptions previously made (SHULL 1911; EAST and HAYES 1912), that factors in the heterozygous condition stimulate development by virtue of their being in that condition, without showing in any way why this should be so.

There is abundant evidence to show that many abnormal characters exist in a naturally cross-pollinated species and that they are recessive to the normal condition. In maize innumerable examples can be cited. In addition to the complete lack of chlorophyll already mentioned, there are also other chlorophyll factors which distinguish yellowish-green plants from normal green plants, just as there are cases of both conditions in other plants, e.g., *Pelargonium* (BAUR 1911). By inbreeding, strains of maize are isolated which are dwarf; some are sterile; some have contorted stems; some fasciated ears. Some are more susceptible to the bacterial wilt disease, and still others have brace roots so poorly developed that they cannot stand upright when the plants become heavy. It is unnecessary to mention more examples, because their occurrence in many kinds of material is familiar to everyone. All the characters cited are recessive, either completely or to a large degree, to the normal condition. More than one of these unfavorable characters may be present together in one inbred strain. No one strain so far known has them all.

Crossing many of these strains of maize together produces perfectly normal F_1 plants. They are normal because the factors which one strain lacks are supplied by the other, and conversely. Because more of the favorable characters are present when the strains are united in F_1 than in either parent, the F_1 is naturally able to attain a greater development. This effect is heterosis.

In the preceding diagrammatic illustration of the way in which heterosis may be brought about it was assumed that all factors had equal effects, that they were evenly distributed in the chromosomes, and that there were no crossovers. This is probably far from describing all the actual conditions. All deviations from this uniformity add to the complexity of the problem. It remains to be seen whether or not the assumption of dominance as an explanation of heterosis will not meet all or most of the requirements raised by all these complicating factors. It is only necessary to consider that a large number of factors is concerned, and that those factors are in most cases fairly evenly distributed among all the chromosomes, and that, in the main, crossovers in some places are balanced by crossovers in others.

Crossing over also provides a means of understanding why certain homozygous individuals (and varieties) may possess a greater number of desirable characters than others. Exceptionally good individuals might be formed by crossing over in heterozygotes occurring in such a manner that all, or a large number of, desirable characters would be combined together eventually in one individual. Such a condition, ac-

cording to the laws of chance, would be exceedingly rare, which is well in accord with the facts.

Without going into all the possibilities which this viewpoint opens up, it is only necessary to say that a way is offered to meet the objections which have been raised against the conception of dominance as a means of accounting for the facts of heterosis as so far known.

There is still the possibility that there may be a stimulus derived from crossing quite apart from hereditary factors. The view presented here simply coördinates the existing knowledge of heredity so as to give a comprehensible view of the way in which heterosis may be brought about.

SUMMARY

1. The phenomenon of increased growth derived from crossing both plants and animals has long been known but never accounted for in a comprehensible manner by any hypothesis free from serious objections.

2. The conception of dominance, as outlined by KEEBLE and PELLEW in 1910 and illustrated by them in height of peas, has had two objections which were: *a*. If heterosis were due to dominance of factors it was thought possible to recombine in generations subsequent to the F_2 all of the dominant characters in some individuals and all of the recessive characters in others in a homozygous condition. These individuals could not be changed by inbreeding. *b*. If dominance were concerned it was considered that the F_2 population would show an asymmetrical distribution.

3. All hypotheses attempting to account for heterosis have failed to take into consideration the fact of linkage.

4. It is shown that, on account of linked factors, the complete dominant or complete recessive can never or rarely be obtained, and why the distributions in F_2 are symmetrical.

5. From the fact that partial dominance of qualitative characters is a universal phenomenon and that abnormalities are nearly always recessive to the normal conditions, it is possible to account for the increased growth in F_1 because the greatest number of different factors are combined at that time.

6. It is not necessary to assume perfect dominance. It is only necessary to accept the conclusion that many factors in the $1n$ condition have more than one-half the effect that they have in the $2n$ condition.

7. This view of dominance of linked factors as a means of accounting for heterosis makes it easier to understand: *a*, why heterozygosis should have a stimulating rather than a depressing or neutral effect; and *b*, why

the effects of heterozygosis should operate throughout the lifetime of the individual, even through many generations of asexual propagation.

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SEX DETERMINATION IN *ANTHOTHIRIPS VERBASCI*

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The mullein thrips is a species that was formerly supposed to reproduce only sexually. Both sexes are abundant; fully formed spermatozoa are produced by the male; and copulation may frequently be observed in nature. Two years ago, however, it was discovered (SHULL 1915) that virgin females also produced offspring. At the time of publication of the paper cited the sex of such parthenogenetically produced offspring was unknown. It could not be stated, therefore, whether the parthenogenesis of *Anthothrips* was of the aphid type, in which both sexes develop from parthenogenetic eggs; or of the honey-bee type, in which fertilized eggs produce females, unfertilized eggs males; or of a third type unlike any species now known.

The experiments here described were designed to solve the problem of the relation of parthenogenesis to sex in this species.

VIRGIN FEMALES PRODUCE ONLY MALES

The experiments that showed that virgin females produce only sons were of two kinds. These two kinds differed only in the time elapsing between the beginning of the experiment and the removal of the parents from the host plant. In some experiments the parents were removed before the first offspring became adult, in others not until adult offspring were present.

Experiments in which the parents were removed while the oldest offspring were still immature

Virgin females were procured by rearing pupae in isolation until they emerged as adults. The sex was ascertained by placing the live insect in a drop of water under a supported cover glass, and examining with a microscope. Only the females were retained. These were placed on young mullein plants that had been reared from seed under cover, and

were protected by lantern globes closed at the top with closely woven cloth. In some experiments only one female was placed on a single plant, in others a number of females were put together on the same plant. All these females were removed before the first offspring became adult. The offspring subsequently removed are recorded in table 1.

TABLE 1

A record of the sex of the offspring of virgin females of Anthothrips verbasci, in experiments in which the parents were removed before any of the offspring became adult.

Number of experiment	Number of females used as parents	Date of beginning of experiment	Date of removal of parents	Offspring	
				Males	Females
93	1	Aug. 28, 1914	Apr. 12	1	0
95	2	Aug. 30, 1914	Apr. 12	18	0
99	5	Sept. 11, 1914	Dec. 5	63	0
100	7	Sept. 14, 1914	Dec. 5	9	0
101	7	Sept. 16, 1914	Apr. 12	8	0
102	9	Sept. 16, 1914	Dec. 5	22	0
129	1	July 5, 1915	July 29	6	0
131	3	July 9, 1915	July 29	68	0
132	3	July 9, 1915	July 29	34	0
133	3	July 12, 1915	July 29	48	0
134	5	July 12, 1915	July 29	60	0
135	5	July 12, 1915	July 29	57	0
145	4	July 14, 1915	July 30	39	0
146	2	July 17, 1915	July 30	18	0
147	5	July 19, 1915	July 30	79	0
149	7	July 19, 1915	July 30	32	0
150	7	July 19, 1915	July 30	53	0
151	8	July 22, 1915	July 30	32	0
163	3	July 29, 1915	Sept. 21	38	0
170	5	July 29, 1915	Sept. 22	3	0
Totals	92			688	0

There is abundant proof in these experiments that unfertilized eggs produce males.

Experiments in which the parents were not removed until the first offspring were adult

These experiments were conducted in every way like those recorded in table 1, except that the parents remained on the host plant until some of the offspring were adult. When adults were subsequently removed from the plant, they may or may not have included the parents, depending on

whether the latter survived. The sex of the thrips removed from such plants is stated in table 2.

TABLE 2

A record of the sex of individuals of Anthothrips verbasci taken from plants on which virgin females had previously been placed. The virgin females were left on the plant until some of the offspring were adult, and may be included in this list with the offspring.

Number of experiment	Number of females used as parents	Date of beginning of experiment	Date of removal of parents	Offspring	
				Males	Females
102a	9	Dec. 5, 1915	June 9	15	3
148	5	July 19, 1915	Sept. 20	61	1
152	5	July 24, 1915	Sept. 20	19	3
153	5	July 24, 1915	Sept. 20	45	3
154	5	July 28, 1915	Sept. 20	47	5
155	6	July 28, 1915	Sept. 20	19	5
167	3	July 29, 1915	Sept. 21	28	2
168	5	July 29, 1915	Sept. 21	85	1
169	5	July 29, 1915	Sept. 22	61	2
177	4	July 30, 1915	Sept. 22	63	1
179	7	July 30, 1915	Sept. 23	12	2
Totals	59			455	28

While some females appear among the adults obtained from these plants, the number of females is in no case greater than the number of female parents with which the experiment was started. It is to be assumed, then, in harmony with the experiments of table 1, that the males in table 2 are the offspring, the females are the mothers.

From the above experiments, in both tables, it is sufficiently well established that unfertilized eggs produce only males.

FEMALES THAT MATE MAY PRODUCE BOTH SEXES

In a series of experiments females were either induced to mate in captivity, or were observed to mate in nature, and were then transferred to mulleins in the greenhouse and kept under cover. In each experiment the female alone was placed on the host plant, and she was removed before any of her offspring became adult. These offspring, on becoming adult, were removed and their sex ascertained. In some experiments they were collected from the host plant only once, in others several times. But in every experiment examination of the offspring ceased before any of their offspring (grandchildren of the original female) could have become adult. The records are certainly, therefore, those of the imme-

diate children only. In some experiments both daughters and sons were produced, in others only sons. Tables 3 and 4 show the sex of the offspring in these experiments, grouped for convenience according to the results.

TABLE 3

A record of the sex of the offspring of females of Anthothrips verbasci which were known to have mated, and subsequently produced both daughters and sons.

Number of experiment	Date of beginning experiment	Offspring	
		Males	Females
97	Sept. 3, 1914	18	2
117	July 5, 1915	52	4
119	July 5, 1915	6	2
120	July 5, 1915	33	3
125	July 5, 1915	5	3
138	July 12, 1915	5	2
139	July 12, 1915	51	7
140	July 12, 1915	2	1
143	July 12, 1915	23	6
144	July 12, 1915	32	7
159	July 28, 1915	31	8
Totals		258	45

TABLE 4

A record of the sex of the offspring of females of Anthothrips verbasci which were known to have mated, and subsequently produced only sons.

Number of experiment	Date of beginning experiment	Offspring	
		Males	Females
118	July 5, 1915	2	0
126	July 5, 1915	3	0
137	July 12, 1915	39	0
141	July 12, 1915	16	0
142	July 12, 1915	43	0
Totals		103	0

In harmony with the results shown in table 1, it is to be assumed that the males in table 4 were produced from unfertilized eggs, notwithstanding their mothers had mated. The occurrence of females among the offspring in table 3 and the production of nothing but males in table 1 indicate that fertilized eggs yield females, at least in part. The paucity of females may be partly accounted for by the fact that the females

mated only once, whereas in nature they may be observed to mate repeatedly.

Support for the conclusion that fertilized eggs yield females, at least in part, and unfertilized eggs always males, is found in the offspring of mixed lots of males and females. Two such lots were maintained for a time to provide a stock of thrips for use in experiments, and to ascertain what would be the sex ratio in the greenhouse under conditions as favorable as possible to repeated mating. Table 5 gives the sex of the adults collected from these two plants at intervals, each collection including all the adults present on the date named.

TABLE 5

*Showing the sex ratio of the offspring produced by a mixed lot of males and females of *Anthothrips verbasci* under conditions favorable to repeated mating.*

Number of experiment	Date of beginning experiment	Dates of collecting adult offspring	Offspring	
			Males	Females
203	June 28, 1916	{ Sept. 9, 1916	6	0
		{ Oct. 4, 1916	18	8
		{ Oct. 23, 1916	16	0
		{ Sept. 9, 1916	1	2
204	June 28, 1916	{ Sept. 30, 1916	0	3
		{ Oct. 15, 1916	0	2
		{ Oct. 24, 1916	25	43
		{ Nov. 23, 1916	15	7

These experiments are cited here as showing that when males are present, females appear among the offspring. The sex ratio and its significance is referred to elsewhere.

ALTERATION OF THE SEX RATIO IN FAMILIES OF FEMALES THAT MATE ONCE

From certain theoretical considerations discussed below, it was important to ascertain the sex ratio of the offspring of a female that had mated, and whether that sex ratio is altered if subsequent matings are prevented. Females that were known to have mated were placed alone upon mulleins. Before any of their offspring became adult, they were transferred to new plants. From this second plant the offspring were removed when they became adult, care being taken not to collect so late that any of the grandchildren might be included. In table 6 the sex ratio of the collection from each plant in these experiments is given.

The occurrence of females on the first plant of each experiment, and their absence from the second plant in most cases, is explained on the

TABLE 6

A record of the sex ratio of the offspring of single females of Anthothrips verbasci, known to have mated, the offspring being collected at intervals as they became adult.

Number of experiment	Date of beginning experiment	Dates of collecting adult offspring	Offspring	
			Males	Females
117	July 5, 1915	Sept. 19,* 1915	37	4
		Sept. 21, 1915	15	0
139	July 12, 1915	Sept. 20,* 1915	26	7
		Sept. 22, 1915	25	0
143	July 12, 1915	Sept. 20,* 1915	7	6
		Sept. 22, 1915	15	0
		Oct. 14, 1915	1	0
144	July 12, 1915	Sept. 20,* 1915	21	6
		Sept. 22, 1915	11	1
159	July 28, 1915	Sept. 21,* 1915	22	8
		Oct. 14, 1915	9	0

* Must have been mature much earlier. Were on the first plant to which the female was transferred.

assumption that the spermatozoa were all allowed to fertilize eggs at first, and that subsequent eggs were unfertilized.

Another experiment not included in table 6 because performed in a slightly different way, bears upon the same theoretical point, and is here recorded separately. In experiment 94, a virgin female and a male were placed together on a plant December 16, 1914. Copulation was not witnessed, but the results indicate that mating occurred. The first offspring became adult shortly before June 18, 1915, on which date all adults were removed. These proved to be 9 males and 27 females, and they may or may not have included the original parents. On June 29 another collection of adult offspring was made, comprising 53 males and 60 females. Further collections were made, but since the grandchildren may have had time to mature before these later lots were collected, the sex ratio of the later collections is of no value in this connection. In the figures given it is worthy of note that the females are in the majority, distinctly so in the first collection. The importance of this fact is indicated elsewhere.

DISCUSSION

From the experiments described it was early established that unferti-

lized eggs of *Anthothrips verbasci* produce only males. I also conclude that fertilized eggs produce only females, but was not forced to this conclusion until consideration of the above experiments left no other assumption probable. By analogy with the honey-bee, it was to be expected that, if parthenogenetic eggs yielded males, fertilized eggs would yield only females. But another analogy with the honey-bee, the degeneration of the male-producing spermatozoa, could not be established. The close relationship of the thrips to the Hemiptera on the one hand and the Orthoptera on the other, lead one to expect two types of spermatozoa, respectively male-producing and female-producing, in the thrips. Moreover, casual observations made upon poorly fixed material showed, in some cell divisions, what appeared to be a lagging chromosome, though I have not verified this observation on better material. However, if two types of spermatozoa are produced, analogy with the honey-bee requires the male-producing type to degenerate. This degeneration I have been unable to see in sections, though the minuteness of the object may account for my failure.

If sex in the thrips is not determined in the same way as in the honey-bee, there seemed but one probable alternative. It appeared possible that unfertilized eggs gave rise to males, and fertilized eggs to both males and females, depending on which type of spermatozoön fertilized the egg. The fact that no case of this kind is yet on record did not warrant the rejection of the hypothesis without consideration.

In the absence of any cytological evidence, the major part of the experiments described above were performed to test the correctness of the two hypotheses just outlined.

If the sex of thrips is determined in the same way as that of the honey-bee, the sex ratio may be anything. If, on the other hand, fertilized eggs yield males as well as females, in equal numbers, because there are two types of spermatozoa, the males must always predominate; for, to the fifty percent of males hatching from fertilized eggs must be added those developing from unfertilized eggs. The latter view also requires that there be two kinds of male, one from parthenogenetic and one from fertilized eggs.

The sex ratio among the offspring of impregnated females, as found in the greenhouse, usually showed a preponderance of males. Tables 3, 5, and 6 afford abundant illustrations. Certain exceptions, however, are crucial. Experiment 94 showed that a female which had every opportunity to mate produced, among her first offspring, 27 females and 9 males. A later collection comprised 60 females and 53 males. Like-

wise, in experiment 204 (table 5), which was started with a mixed lot of males and females, the first four collections of offspring showed a preponderance of females. The marked excess of females in these two cases seems to exclude the hypothesis that males arise from all parthenogenetic and half the fertilized eggs, because by that hypothesis there could never be, except by rare chance, a large majority of females. Furthermore, no evidence has been obtained that there are males of two kinds.

It seems necessary to conclude, therefore, that sex in this species of thrips is determined as in the honey-bee. Unfertilized eggs always produce males, fertilized eggs always females. Moreover, there is, as in the honey-bee, some means of withholding the spermatozoa, so that unfertilized eggs may be laid even while spermatozoa are present. Evidence that this is true is found in experiment 144 (table 6). The offspring produced on the first plant, which were collected September 20, included a large proportion of males. Yet, from the second plant, to which the mother was transferred July 30, one female and eleven males were taken September 22. The one female was taken as a pupa on that date and was allowed to emerge as an adult in the laboratory. The spermatozoön which fertilized the egg from which she developed must have been withheld while at least 21 earlier eggs were laid without fertilization.

This statement of the method of sex determination in thrips is made for only one species, *Anthothrips verbasci*. It is not improbable that it is true for some other species; but it can hardly be applied to species in which there are very few males, and certainly not to those in which there are no males. In *Thrips tabaci*, for example, males are rare (SHULL 1914); likewise in *Anaphothrips striatus* in certain regions (HINDS 1902). In these species, and others like them in this respect, rarity of males at any given time should, if sex were determined as in the mullein thrips, result in the parthenogenetic development of most of the eggs laid; and hence in an abundance of males in the next generation. The long periods of time over which the sex ratio of such species has been observed, preclude the possibility of a fluctuation as extreme as that mentioned. In *Thrips tabaci*, therefore, and in *Anaphothrips striatus* in regions where males are rare, the occasional males must arise through some change in the eggs (perhaps in their maturation), as in the aphids and phylloxerans.

That *Anthothrips verbasci* is not, however, the only thrips in which sex is dependent upon fertilization, is indicated by peculiarities of the sex ratio which were formerly very puzzling. In *Chirothrips manicatus*,

a species living on timothy, bluegrass and other grasses, the sex ratio has been observed (SHULL 1914) to fluctuate enormously within short periods of time. At Douglas Lake, Michigan, this species was observed at intervals in a small island of timothy in a thicket of bushes and small trees. As *Chirothrips* is not a ready flier, and shows little inclination even to crawl, the phenomenon about to be described can hardly have been due to migration. In this island of timothy the adult specimens collected were at first mostly females. Then adults practically disappeared for a time. A week or two later adults were again fairly abundant, but nearly all were males. A similar change in the sex ratio has since been observed in the outskirts of Ann Arbor, and I am told by Mr. C. B. WILLIAMS that he has seen the same occurrence in England. In the light of the experiments on *Anthothrips verbasci*, I think we may interpret the peculiar changes in the sex ratio of *Chirothrips manicatus*. The mothers of the adults collected were probably impregnated, and the first offspring were mostly females. For some reason mating did not occur again, and subsequent eggs developed parthenogenetically, producing males. *Chirothrips* is not as easy to rear under guarded conditions as *Anthothrips*, and experiments intended to verify or refute the above hypothesis failed. The only other explanation of the peculiarities of the sex ratio in *Chirothrips* that seems plausible is that perhaps the males require longer to develop than the females. From my experience with other insects I should expect just the reverse. I assume, therefore, that sex in *Chirothrips manicatus* is probably dependent on fertilization, just as in *Anthothrips verbasci*.

One more question is raised, but not answered, by the results of the experiments with *Anthothrips*. Why are the females more abundant than males in nature, whereas in the insectary the males have been found to be in the majority? It may be that the conditions of the greenhouse are not favorable to repeated copulation. Or the males may be short-lived, a fact which would not be detected in the experiments, since adults were usually still young when collected. Or the males may migrate more readily than the females. These hypotheses could readily be tested by experiment.

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SOME APPLICATIONS OF MATHEMATICS TO BREEDING PROBLEMS

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INTRODUCTION

In a recent paper Professor JENNINGS (1916) has given formulae for the calculation of the results of various systems of breeding in which a single Mendelian trait is in question. It seems that JENNINGS'S method gave him no absolute assurance of the correctness of his formulae. To quote from his paper (1916, page 62),

"After a law or regular series is obtained that fits the first five or six generations, the law is applied to give the results for three or four generations more. These results are then tested by the actual detailed working out (symbolic formation of gametes and their mating, etc.) for these same later generations; if the formula has given the correct results, it is assumed to be a general formula."

Again (1916, page 61),

"I am compelled, therefore, in most cases, to content myself with giving the actual formulae, leaving their correctness to the test of time."

It is the purpose of this paper, first, to give some examples to show how a method of mathematical repetition can be used to suggest formulae and how mathematical induction can be used to establish a formula when once suggested; second, to express the n th term of series in JENNINGS's table 1, (1916, page 54) as a function of n ; third, to solve the problem of inbreeding by brother and sister mating. This paper deals only with a single pair of typical Mendelian factors.

PART I. APPLICATIONS OF THE METHODS OF MATHEMATICAL INDUCTION AND REPETITION

1. *Random mating in a general population*

Consider the problem of random mating in a population consisting of $r AA + s Aa + t aa$. The fundamental method of considering all possible crosses gives the results stated by JENNINGS (1916, page 65) for the first generation:

$$1) \quad (s + 2r)^2 AA + 2(s + 2r)(s + 2t)Aa + (s + 2t)^2 aa.$$

It should be stated once for all that it is only the relative magnitudes of the coefficients of AA , Aa and aa which are of interest. It has been shown¹ that 1) gives the result for all following generations. A proof will be given here to illustrate a method which is quite valuable for other problems in breeding.

To get the composition of the second generation, one should note that he has merely a repetition of the problem of getting the composition of the first generation. We have to consider the problem of random mating in a population consisting of $R AA + S Aa + T aa$, in which

$$2) \quad R = (s + 2r)^2, S = 2(s + 2r)(s + 2t), T = (s + 2t)^2.$$

It is needless to repeat the work involved in obtaining expression 1). We read from 1) immediately that the second generation will have the composition

$$3) \quad (S + 2R)^2 AA + 2(S + 2R)(S + 2T)Aa + (S + 2T)^2 aa.$$

To find what this means in terms of r , s , t , we substitute the values of R , S , T from 2) into the expression 3). This gives the composition

$$AA = 16(r + s + t)^2(s + 2r)^2.$$

$$Aa = 16(r + s + t)^2 2(s + 2r)(s + 2t).$$

$$aa = 16(r + s + t)^2(s + 2t)^2.$$

For want of a better name this process is called "mathematical repeti-

¹ This has been proved by WENTWORTH and REMICK (1916) who state that JENNINGS also had the result.

tion." Omitting the common factor, $16(r + s + t)^2$, which has nothing to do with the proportions involved, we have the same composition for the second generation that we had for the first.

We can read from this result more than a conclusion regarding the second generation. We can say that random mating in any population of composition 1) results in another generation of the same composition. Thus for our original problem, we have the conclusion that after the first random mating the proportions in the population are fixed and are given by expression 1).

2. *A special case of assortative mating*

This example is to illustrate how mathematical induction can be used to test the accuracy of a formula when once suggested. Consider the problem of assortative mating, dominants with dominants, recessives with recessives. Beginning with a cross between AA and aa , and following this by assortative mating for n generations, JENNINGS (1916, page 66) gives the resultant composition as follows:

$$4) \quad (n + 1)AA + 2Aa + (n + 1)aa.$$

If this composition is correct for a particular value of n , and assortative mating occurs in the population it represents, the next generation should show a composition obtained from 4) by replacing n with $n + 1$. Conversely, if assortative mating in the population 4) gives a population of composition obtained by replacing n by $n + 1$ in 4), and if our original problem gives the distribution 4) for $n = 1$, then the formula 4) holds for all values of n . The most elementary methods show that 4) holds for $n = 1$. Then to complete the proof it is only necessary to show that assortative mating in a population 4) results in a population of composition obtained by replacing n by $n + 1$ in 4); i.e.,

$$5) \quad (n + 2)AA + 2Aa + (n + 2)aa.$$

In assortative mating the AA and Aa individuals mate at random while the aa individuals mate with like kind. Out of every $2n + 4$ children, $n + 3$ will come from dominant parents, the remaining $n + 1$ coming from recessive parents. The crosses among the dominants will be in the proportions

$$(n + 1)^2 AA \times AA, 4(n + 1) AA \times Aa, 4 Aa \times Aa.$$

We shall use the notation (a, b, c) to indicate a individuals of type AA , b of type Aa and c of type aa . Then the three crosses noted will produce individuals in the following proportions:

$$\begin{array}{rcl}
 & (a, & b, & c) \\
 (n+1)^2 AA \times AA & = & ((n+1)^2, & 0, & 0). \\
 4(n+1)AA \times Aa & = & (2(n+1), & 2(n+1), & 0). \\
 4Aa \times Aa & = & (1, & 2, & 1). \\
 \text{Totals} & = & ((n+2)^2, & 2(n+2), & 1).
 \end{array}$$

Then the $(n+1)$ th generation consists of individuals in the following proportions:

$$\begin{aligned}
 AA &= \frac{(n+2)^2}{(n+3)^2} \cdot \frac{n+3}{2n+4}; \quad Aa = \frac{2(n+2)}{(n+3)^2} \cdot \frac{n+3}{2n+4}; \\
 aa &= \frac{1}{(n+3)^2} \cdot \frac{n+3}{2n+4} + \frac{n+1}{2n+4} = \frac{(n+2)^2}{(n+3)(2n+4)}
 \end{aligned}$$

Removing the common factor $1/[2(n+3)]$ we have

$$(n+2)AA + 2Aa + (n+2)aa,$$

which is identical with expression 5) as was desired.

3. Assortative mating in a general population

As a final example illustrating both methods, consider the more general problem of assortative mating of the population

$$rAA + sAa + taa.$$

Detailed examination of the crosses involved gives the result stated by JENNINGS (1916, page 67) for the first generation,

$$6) \quad (2r+s)^2 AA + 2s(2r+s)Aa + (s^2 + 4rt + 4st)aa.$$

The problem is now really simpler than was the special case considered above. To get the composition of the second generation we need not consider the crosses involved at all. If we set

$$7) \quad (2r+s)^2 = R, \quad 2s(2r+s) = S, \quad s^2 + 4rt + 4st = T,$$

expression 6) can be written

$$RAA + SAa + Taa.$$

We seek the result of assortative mating in this population and it is evident that it is only necessary to write expression 6) with large letters. The second generation has the composition,

$$8) \quad (2R+S)^2 AA + 2S(2R+S)Aa + (S^2 + 4RT + 4ST)aa.$$

To interpret this we must replace R, S, T by their values in r, s, t from equations 7).

$$(2R+S)^2 = 4(2r+s)^2(2r+2s)^2.$$

$$2S(2R+S) = 4(2r+s)^2 2s(2r+2s).$$

$$S^2 + 4RT + 4ST = 4(2r+s)(2r+2s)(2s^2 + 4rt + 6st).$$

Omitting the common factor $4(2r + s)(2r + 2s)$, we have for the second generation

$$9) \quad (2r + s)(2r + 2s)AA + 2s(2r + s)Aa + (2s^2 + 4rt + 6st)aa.$$

This, or at least one more repetition of the process, suggests that the n th generation will have the composition²

$$10) \quad (2r + s)(2r + ns)AA + 2s(2r + s)Aa + [ns^2 + 4rt + 2(n + 1)st]aa.$$

Inspection shows that this formula holds for $n = 1$ and $n = 2$. If we assume 10) thinking of n as fixed, and show that assortative mating in such a population gives a generation whose composition is obtained by replacing n by $n + 1$ in 10), then we shall know that 10) holds for all values of n . To do this let

$R = (2r + s)(2r + ns)$; $S = 2s(2r + s)$; $T = ns^2 + 4rt + 2(n + 1)st$, and form expression 6) in the large letters; i.e., the expression 8) with our present meaning for R, S, T . This process gives for the proportions in the $(n + 1)$ th generation.

$$AA = 4(2r + s)^2[2r + (n + 1)s]^2.$$

$$Aa = 4(2r + s)^2 \cdot 2s[2r + (n + 1)s].$$

$$aa = 4(2r + s)[2r + (n + 1)s][n + 1)s^2 + 4rt + 2(n + 2)st].$$

Dividing by the common factor $4(2r + s)[2r + (n + 1)s]$ the proportions become,

$$(2r + s)[2r + (n + 1)s]AA + 2s(2r + s)Aa + [(n + 1)s^2 + 4rt + 2(n + 2)st]aa.$$

Inspection shows that these results may be obtained by replacing n by $n + 1$ in expression 10).

It should be of interest to note that as n increases indefinitely the proportions in 10) approach the proportions in

$$(2r + s)AA + 0 Aa + (2t + s)aa.$$

These examples should show, first that the method of mathematical repetition can be used to simplify the work of calculating the composition of higher generations; second, that the method of mathematical induction can be used to prove or disprove a general formula for the composition of the n th generation when it has once been suggested.

PART II. GENERAL TERMS OF JENNINGS'S SERIES

In table 1 JENNINGS (1916, page 54) gives twenty terms of each of several series which present themselves in breeding problems. For series

² This result was obtained by WENTWORTH and REMICK (1916).

B, C, D and E he gives the n th term as a function of n . It may be desirable to have the n th term of his other series (lettered from F to M). Inspection shows that only two of these are independent and if we can express the n th term of each of them, the others come immediately. The derivation of these two n th terms will be given next and then the n th term of each series will be written down.

1. Derivation of the n th term of the Fibonacci series

The Fibonacci series F is defined by its first two terms, $F_0 = 0$, $F_1 = 1$, and the recurrence relation $F_n = F_{n-1} + F_{n-2}$. In mathematical language we have to solve the homogeneous recurrence equation

$$11) \quad F_n - F_{n-1} - F_{n-2} = 0$$

with the initial conditions, $F_0 = 0$ and $F_1 = 1$. It is well known that C^n is a solution of 11), where C is a root of $C^2 - C - 1 = 0$; i.e., $C = (1 \pm \sqrt{5})/2$. Then $[(1 + \sqrt{5})/2]^n$ and $[(1 - \sqrt{5})/2]^n$ are solutions of 11) and any solution can be put in the form

$$12) \quad F_n = [K_1(1 + \sqrt{5})^n + K_2(1 - \sqrt{5})^n]/2^n.$$

We wish to determine the constants K_1 and K_2 so that $F_0 = 0$ and $F_1 = 1$. Setting $n = 0$ and $n = 1$ in equation 12), we have

$$13) \quad F_0 = K_1 + K_2 = 0.$$

$$14) \quad F_1 = [K_1(1 + \sqrt{5}) + K_2(1 - \sqrt{5})]/2 = 1.$$

From 13), $K_1 = -K_2$. Substituting in 14),

$$F_1 = K_1[1 + \sqrt{5} - (1 - \sqrt{5})]/2 = 1.$$

$$K_1 = 1/\sqrt{5}; K_2 = -1/\sqrt{5}; \text{ and}$$

$$15) \quad F_n = [(1 + \sqrt{5})^n - (1 - \sqrt{5})^n]/[\sqrt{5} \cdot 2^n].$$

The rather complicated appearance of this formula may make it seem useless. If one desires only a few of the early terms in the series, it would most certainly not be advisable to use this formula. But suppose you want the 100th term. By using logarithms it is about as easy to get the 100th term with all desirable accuracy from this formula 15) as it is to get the tenth term, and no time need be spent calculating the first 99 terms.

The formula 15) for the Fibonacci series enables us to prove the following important

THEOREM: *As n increases indefinitely, the n th term of the Fibonacci series divided by 2^n approaches zero as a limit.*

Symbolically stated, the theorem is

$$16) \quad \lim_{n \rightarrow \infty} F_n/2^n = 0.$$

Writing in the value of F_n this becomes

$$\lim_{n \rightarrow \infty} \frac{(1 + \sqrt{5})^n - (1 - \sqrt{5})^n}{\sqrt{5} \cdot 4^n} = 0.$$

The proof consists in noting that $(1 + \sqrt{5})/4$ and $(1 - \sqrt{5})/4$ are proper fractions and that as a proper fraction is raised to higher and higher powers, the result approaches zero as a limit. As an immediate corollary we have that if C_1 and c_2 are constants,

$$\lim_{n \rightarrow \infty} C_1 F_n / 2^{n+c_2} = 0.$$

This follows because $C_1/2^{c_2}$ is a constant, say C_3 , and we have

$$\lim_{n \rightarrow \infty} \frac{C_3 F_n}{2^n} = C_3 \lim_{n \rightarrow \infty} \frac{F_n}{2^n} = 0.$$

2. Derivation of series G

The second series which it is necessary to consider is defined by the recurrence $G_n = 2^{n-1} - G_{n-1}$, together with the initial condition $G_0 = 0$. We have to solve the non-homogeneous recurrence

$$17) \quad G_n + G_{n-1} = 2^{n-1}$$

subject to the condition $G_0 = 0$. The most general solution is the sum of the general solution of the homogeneous equation

$$18) \quad G_n + G_{n-1} = 0$$

and any particular solution of equation 17). The general solution of 18) is $K(-1)^n$ where K is a solution of $C + 1 = 0$; i.e., $K(-1)^n$. A particular solution of equation 17) is $G_n = 2^n/3$.

The general solution of 17) is therefore

$$19) \quad G_n = K(-1)^n + 2^n/3.$$

We wish to determine K so that $G_0 = 0$. Setting $n = 0$ in 19), we have

$$G_0 = K + 1/3. \therefore K = -1/3 \text{ and}$$

$$20) \quad G_n = [2^n - (-1)^n]/3.$$

The value of a formula for G_n is particularly apparent in an example given by JENNINGS (1916, page 80). The series $G_n \cdot G_{n+1}/2^{2n-1}$ is needed. Substituting the value of G_n and G_{n+1} this fraction is

$$\frac{1}{9} \left[\frac{2^{2n+1} - (-2^n) - 1}{2^{2n-1}} \right] = \frac{4}{9} - \frac{(-2)^n + 1}{9 \cdot 2^{2n-1}}.$$

From this expression, the various terms of the series can be calculated readily, independently, and without recourse to any complicated rule, and the limit approached as n increases indefinitely is apparent.

3. The n th terms of series in JENNINGS's table

Using the values of F_n and G_n we can write down the following set of n th terms for JENNINGS's series:

$$F_n = \frac{(1 + \sqrt{5})^n - (1 - \sqrt{5})^n}{\sqrt{5} \cdot 2^n}; G_n = \frac{1}{3} [2^n - (-1)^n]; B_n = 2^n.$$

$$H_n = G_n - F_n = \frac{1}{3} [2^n - (-1)^n] + \frac{(1 - \sqrt{5})^n - (1 + \sqrt{5})^n}{\sqrt{5} \cdot 2^n}.$$

$$I_n = B_n - G_n - F_n = \frac{2^{n+1} + (-1)^n}{3} + \frac{(1 - \sqrt{5})^n - (1 + \sqrt{5})^n}{\sqrt{5} \cdot 2^n}.$$

$$J_n = B_n - F_{n+1} = 2^n + \frac{(1 - \sqrt{5})^{n+1} - (1 + \sqrt{5})^{n+1}}{\sqrt{5} \cdot 2^{n+1}}.$$

$$K_n = B_n - F_{n+2} = 2^n + \frac{(1 - \sqrt{5})^{n+2} - (1 + \sqrt{5})^{n+2}}{\sqrt{5} \cdot 2^{n+2}}.$$

$$L_n^3 = B_n - G_{n-1} - F_{n-1} = \frac{5 \cdot 2^{n-1} + (-1)^{n-1}}{3} + \frac{(1 - \sqrt{5})^{n-1} - (1 + \sqrt{5})^{n-1}}{\sqrt{5} \cdot 2^{n-1}}.$$

$$M_n = 3 B_n - F_{n+2} = 3 \cdot 2^n + \frac{(1 - \sqrt{5})^{n+2} - (1 + \sqrt{5})^{n+2}}{\sqrt{5} \cdot 2^{n+2}}.$$

Incidentally it may be noted that E_n , given by JENNINGS as $2^{n-1} + 2^{n-2} - 1$ can be written in the slightly more compact form, $E_n = 3 \cdot 2^{n-2} - 1$.

PART III. BROTHER AND SISTER MATING

I. Results in random brother and sister mating

Given a family consisting of $r AA + s Aa + t aa$, what is the composition of the n th generation if mating is restricted to random mating between brothers and sisters? Special cases of this problem have been considered by JENNINGS (1916) and PEARL (1914).

For the benefit of those who do not care to follow the details of the development, the results will be stated first. The n th generation, i.e., the generation resulting from the n th brother and sister mating, has the following composition:

$AA = [1 + K_2 - T_n]/2$; $Aa = T_n$; $aa = [1 - K_2 - T_n]/2$, in which $T_n = [s K F_{n+1} + (rs + st + 4rt)F_n]/K^2 \cdot 2^n$; $K_2 = (r - t)/K$; $K = r + s + t$; and F_n is the general term of the Fibonacci series.

* By what is evidently a slip, JENNINGS writes F_{n+1} in this equation for F_{n-1} .

2. *Development of above results*

Three types of individuals are involved, AA , Aa and aa . The different possible crosses of individuals of these types together with the composition of the resulting families are given below. The notation (a, b, c) means that individuals of the types AA , Aa , aa appear in numbers proportional to a, b, c .

Kind of cross	Composition of resulting family	Letter indicating type of family
$AA \times AA$	(1, 0, 0)	o
$AA \times Aa$	($\frac{1}{2}$, $\frac{1}{2}$, 0)	p
$AA \times aa$	(0, 1, 0)	q
$Aa \times Aa$	($\frac{1}{4}$, $\frac{1}{2}$, $\frac{1}{4}$)	r
$Aa \times aa$	(0, $\frac{1}{2}$, $\frac{1}{2}$)	u
$aa \times aa$	(0, 0, 1)	v

It is useful to keep track of these six kinds of families. Let $o_n, p_n, q_n, r_n, u_n, v_n$ be the relative numbers of families of the various kinds in the order given above. If we can calculate o_n, \dots, v_n we can readily find the numbers of AA, Aa, aa individuals in the n th generation.

a. *Development of the formulae for $o_n, p_n, q_n, r_n, u_n, v_n$*

To find o_n , for instance, we examine the source of the families in the n th generation of the type o . All the children of families of type o in the $(n-1)$ th generation will be in families of type o , since AA individuals only are concerned. One-fourth of the families which consist of children of families of type p in the $(n-1)$ th generation will be of type o and $1/16$ of the families which are children of families of type r in the $(n-1)$ th generation will be of type o . Thus we have that⁴

$$21) \quad o_n = o_{n-1} + p_{n-1}/4 + r_{n-1}/16.$$

Similar considerations give

$$22) \quad p_n = p_{n-1}/2 + r_{n-1}/4.$$

$$23) \quad q_n = r_{n-1}/8.$$

$$24) \quad r_n = p_{n-1}/4 + q_{n-1} + r_{n-1}/4 + u_{n-1}/4.$$

$$25) \quad u_n = u_{n-1}/2 + r_{n-1}/4.$$

$$26) \quad v_n = v_{n-1} + u_{n-1}/4 + r_{n-1}/16.$$

The problem before us is to solve this system of recurrence relations.

⁴ PEARL (1914) had these equations, except that in the case he considered, $o_n = v_n$; $p_n = u_n$. The notation here used was used by PEARL.

We first set

$$27) \quad p_n - u_n = y_n, \quad \text{and}$$

$$28) \quad o_n - v_n = x_n.$$

Then from equations 22) and 25),

$$29) \quad y_n = y_{n-1}/2, \quad \text{and similarly}$$

$$30) \quad x_n = x_{n-1} + y_{n-1}/4 \quad \text{and the above system, 21)-26), may be replaced by the following system:}$$

$$21') \quad o_n = o_{n-1} + p_{n-1}/4 + r_{n-1}/16.$$

$$22') \quad p_n = p_{n-1}/2 + r_{n-1}/4.$$

$$23') \quad r_n = r_{n-1}/4 + r_{n-2}/8 + p_{n-1}/2 - y_{n-1}/4.$$

$$24') \quad y_n = y_{n-1}/2.$$

$$25') \quad x_n = x_{n-1} + y_{n-1}/4.$$

Equation 24') may be written

$$2y_n - y_{n-1} = 0.$$

The most general solution of this equation is

$$31) \quad y_n = K_1/2^n, \text{ in which } K_1 \text{ is an arbitrary constant. Then equation 25')} becomes$$

$$x_n - x_{n-1} = K_1/2^{n+1}.$$

The most general solution of this equation is

$$32) \quad x_n = K_2 - K_1/2^{n+1}, \quad K_2 \text{ being an arbitrary constant.}$$

From equation 22')

$$33) \quad \begin{cases} r_{n-1} = 4p_n - 2p_{n-1}, \\ r_{n-2} = 4p_{n-1} - 2p_{n-2}, \\ r_n = 4p_{n+1} - 2p_n. \end{cases}$$

Substituting these values of r_n, r_{n-1}, r_{n-2} , in equation 23') and using equation 31) gives the equation

$$34) \quad 16p_{n+1} - 12p_n - 2p_{n-1} + p_{n-2} = -K_1/2^{n-1}.$$

The corresponding algebraic equation is $16c^3 - 12c^2 - 2c + 1 = 0$;

the roots are $c = 1/4$; $c = (1 + \sqrt{5})/4$; $c = (1 - \sqrt{5})/4$. Then the most general solution of the homogeneous equation

$$16p_{n+1} - 12p_n - 2p_{n-1} + p_{n-2} = 0 \text{ is}$$

$$[K_3(1 + \sqrt{5})^n + K_4(1 - \sqrt{5})^n + K_5]/4^n,$$

in which K_3, K_4 and K_5 are arbitrary constants. A particular solution of the non-homogeneous equation 34) is $K_1/2^{n+1}$. Therefore the general solution of equation 34) is

$$35) \quad p_n = \frac{K_1}{2^{n+1}} + \frac{K_3(1 + \sqrt{5})^n + K_4(1 - \sqrt{5})^n + K_5}{4^n}$$

Let $P_n = K_3(1 + \sqrt{5})^n + K_4(1 - \sqrt{5})^n$.

Then 35) may be written,

$$36) \quad p_n = K_1/2^{n+1} + (P_n + K_5)/4^n.$$

From $y_n = p_n - u_n$, we have $u_n = p_n - y_n = p_n - K_1/2^n$.

$$37) \quad u_n = -K_1/2^{n+1} + (P_n + K_5)/4^n.$$

From 33) $r_n = 4p_{n+1} - 2p_n$. A little algebraic reduction shows that this becomes

$$38) \quad r_n = [4P_{n-1} - K_5]/4^n.$$

Since $q_n = r_{n-1}/8$, we have

$$39) \quad q_n = (4P_{n-2} - K_5)/2 \times 4^n.$$

By direct substitution one can verify that

$$P_n - 2P_{n-1} - 4P_{n-2} = 0.$$

Using this equation, q_n may be written

$$40) \quad q_n = [P_n - 2P_{n-1} - K_5]/2 \times 4^n.$$

Finally, to get o_n and v_n we note that since $o_n \dots \dots v_n$ are only proportional to the numbers of families of different types, it will simplify the problem to choose them so that,

$$o_n + p_n + q_n + r_n + u_n + v_n = 1.$$

Then $o_n + v_n = 1 - (p_n + q_n + r_n + u_n)$.

From equation 32) we have that

$$o_n - v_n = K_2 - K_1/2^{n+1}.$$

Solving the last two equations for o_n and v_n ,

$$41) \quad o_n = -K_1/2^{n+2} + \frac{K_2 + 1}{2} - \frac{1}{2}(p_n + q_n + r_n + u_n).$$

$$42) \quad v_n = K_1/2^{n+2} - \frac{K_2 - 1}{2} - \frac{1}{2}(p_n + q_n + r_n + u_n).$$

Substituting the values of p_n, q_n, r_n, u_n from equations 36), 37), 38), 40) into equations 41), 42) gives,

$$43) \quad o_n = \frac{1 + K_2}{2} - \frac{K_1}{2^{n+2}} - \frac{5P_n + 6P_{n-1} + K_5}{4^{n+1}}.$$

$$44) \quad v_n = \frac{1 - K_2}{2} + \frac{K_1}{2^{n+2}} - \frac{5P_n + 6P_{n-1} + K_5}{4^{n+1}}.$$

The constants K_1, \dots, K_5 are to be found in terms of the initial conditions; in our problem they are functions of r, s, t . To determine them we need the values of $o_1, p_1, q_1, r_1, u_1, v_1$. Considering the possible crosses involved in mating the family $rAA + sAa + taa$ and using the notation $K = r + s + t$, we find that

$$o_1 = \frac{r^2}{K^2}; p_1 = \frac{2rs}{K^2}; q_1 = \frac{2rt}{K^2};$$

$$r_1 = \frac{s^2}{K^2}; u_1 = \frac{2st}{K^2}; v_1 = \frac{t^2}{K^2}.$$

To evaluate K_1 we note from equation 31) that $y_1 = K_1/2$. Also $y_1 = p_1 - u_1$ by definition. Then $K_1 = 2y_1 = 2(p_1 - u_1)$ and substituting for p_1, u_1 ,

$$45) \quad K_1 = \frac{4s(r-t)}{K^2}.$$

From equation 32), $K_2 = x_1 + K_1/4 = o_1 - v_1 + K_1/4$; and substituting for o_1, v_1 ,

$$46) \quad K_2 = \frac{r-t}{K}.$$

More complicated work of the same nature gives for the remaining constants,

$$47) \quad K_3 = \frac{(1 + \sqrt{5})s}{5K} + \frac{(1 - \sqrt{5})}{5K^2} (s^2 - 4rt).$$

$$48) \quad K_4 = \frac{(1 - \sqrt{5})s}{5K} + \frac{(1 + \sqrt{5})}{5K^2} (s^2 - 4rt).$$

$$49) \quad K_5 = \frac{4}{5K^2} [s(2r - s + 2t) - 8rt].$$

It should be noted that we have here five constants $K_1 \dots K_5$ expressed in terms of three initial numbers r, s, t . This indicates that our method is useful for a more general problem than the one to which it is here applied. This is shown clearly by expressing $K_1 \dots K_5$ in terms of o_1, p_1, \dots, v_1 as follows:

$$K_1 = 2(p_1 - u_1); K_2 = o_1 - v_1 + (p_1 - u_1)/2.$$

$$K_3 = [(1 + \sqrt{5})(p_1 + u_1) + 4(\sqrt{5} - 1)q_1 + 4r_1]/10.$$

$$K_4 = [(1 - \sqrt{5})(p_1 + u_1) - 4(\sqrt{5} + 1)q_1 + 4r_1]/10.$$

$$K_5 = 4[p_1 + u_1 - 4q_1 - r_1]/5.$$

With this set of values of $K_1 \dots K_5$ our formulae will give the composition of the population after $n - 1$ brother and sister matings starting with families of the six special types in numbers proportional to $o_1, p_1, q_1, r_1, u_1, v_1$.

b. Proportions of the three types of individuals in the n th generation

The final results desired are the numbers giving the proportions of

AA , Aa , aa individuals in the n th generation. It is readily seen that they are⁶

$$AA = o_n + p_n/2 + r_n/4.$$

$$Aa = (p_n + r_n + 2q_n + u_n)/2.$$

$$aa = r_n/4 + u_n/2 + v_n.$$

Substituting the values of $o_n \dots v_n$,

$$50) \quad AA = \frac{1 + K_2}{2} - \frac{3P_n + 2P_{n-1}}{4^{n+1}}.$$

$$51) \quad Aa = \frac{3P_n + 2P_{n-1}}{2 \times 4^n}.$$

$$52) \quad aa = \frac{1 - K_2}{2} - \frac{3P_n + 2P_{n-1}}{4^{n+1}}.$$

The expression $3P_n + 2P_{n-1}$ which enters these three equations is

$$3P_n + 2P_{n-1} = \frac{\sqrt{5}}{2} [K_3(1 + \sqrt{5})^{n+1} - K_4(1 - \sqrt{5})^{n+1}].$$

It is instructive to get the proportions in 50), 51), 52) in another form by substituting the values of K_3 and K_4 from equations 47) and 48). This gives

$$Aa = \frac{1}{2^n} \left[\frac{s F_{n+2}}{K} - \frac{s^2 - 4rt}{K^2} F_n \right].$$

in which F_n is the n th term of the Fibonacci series. Since $F_{n+2} = F_{n+1} + F_n$,

$$53) \quad Aa = [sK F_{n+1} + (rs + st + 4rt)F_n] / [2^n \cdot K^2].$$

in which $K = r + s + t$.

From this form we can read the following results:

1. If the numbers representing the proportions of Aa individuals in successive generations be written with 2^n in the denominators, the numerators will satisfy the recurrence,

$$N_n = N_{n-1} + N_{n-2}.$$

2. If $s = 0$ or $s^2 = 4rt$, and the denominators are chosen as $2^n K^2 / (s^2 - 4rt)$ or $2^n K/s$, the numerators will be terms of the Fibonacci series.

3. As the number of generations increases, the proportion of heterozygous individuals approaches zero regardless of the values of r, s, t .

4. As the number of generations increases, the ratio of AA to aa indi-

⁶ PEARL (1914) had this result for AA but seems to have erred in getting the numbers for Aa . In the case he considered, $o_n = v_n$ and $p_n = u_n$.

viduals approaches $(2r + s)/(2t + s)$, which is the same as the ratio of A and a gametes in the original family.

c. Illustrative example

As a check on these formulae, and to illustrate their application, let us take a special case considered by JENNINGS (1916). Let AA and aa be crossed and assume brother and sister mating thereafter. The children of the original cross are all of type Aa . It is with crosses of these individuals that our problem begins. We therefore have $r = t = 0$; $s = 1$. Substituting in equations 45) — 49),

$$K_1 = K_2 = 0; K_3 = K_4 = 2/5; K_5 = -4/5.$$

Substituting these values of the constants into equations 50), 51), 52),

$$\text{and using the notation of part II, } F_n = [(1 + \sqrt{5})^n - (1 - \sqrt{5})^n] / \sqrt{5} \cdot 2^n,$$

$$AA = 1/2 - F_{n+1}/2^{n+1}; Aa = F_{n+1}/2^n;$$

$$aa = 1/2 - F_{n+1}/2^{n+1}.$$

These results agree with JENNINGS's series.

3. Assortative brother and sister mating

Given a family consisting of $rAA + sAa + taa$, what is the composition of the n th generation if mating is restricted (1) to brothers with sisters and (2) to dominants with dominants and recessives with recessives?

To derive the recurrence relations upon which the solution of this problem depends we note:

a) Families of type q will not appear since they arise only by a cross between AA and aa .

b) Families of type u will not appear since they arise only by a cross between Aa and aa .

c) Random mating will occur in families of types o, p, v .

d) Assortative mating will occur in families of type r , $3/4$ of the resulting families being of type o, p, r , in the proportion 1:4:4 and $1/4$ being of the type v .

These considerations lead to the following equations:

$$54) \quad o_n = o_{n-1} + \frac{p_{n-1}}{4} + \frac{r_{n-1}}{12}.$$

$$55) \quad p_n = \frac{p_{n-1}}{2} + \frac{r_{n-1}}{3}.$$

$$56) \quad r_n = \frac{p_{n-1}}{4} + \frac{r_{n-1}}{3}.$$

$$57) \quad v_n = v_{n-1} + \frac{r_{n-1}}{4}.$$

The problem of solving this system of equations is very similar to the problem considered above in studying random brother and sister mating. Using the notation

$$P_n = K_1(5 + \sqrt{13})^n + K_2(5 - \sqrt{13})^n,$$

the solution takes the form,

$$58) \quad o_n = 1 - K_3 - 3 P_{n+1/2} \times 12^{n+1}.$$

$$59) \quad p_n = P_n/12^n.$$

$$60) \quad r_n = (P_{n+1} - 6P_n)/4 \times 12^n.$$

$$61) \quad v_n = K_3 - (P_{n+1} - 4P_n)/8 \times 12^n.$$

The proportions of the three types of individuals in the n th generation are given by

$$62) \quad AA = o_n + \frac{p_n}{2} + \frac{r_n}{4} = 1 - K_3 - \frac{P_{n+1} - 2P_n}{16 \cdot 12^n}.$$

$$63) \quad Aa = \frac{p_n + r_n}{2} = \frac{P_{n+1} - 2P_n}{8 \cdot 12^n}.$$

$$64) \quad aa = v_n + \frac{r_n}{4} = K_3 - \frac{P_{n+1} - 2P_n}{16 \cdot 12^n}.$$

We have to determine the constants K_1 , K_2 , K_3 in terms of the initial numbers r , s , t . First, substituting $n = 1$ in equations 58), 59), 60), 61), and solving,

$$65) \quad K_1 = 2[(\sqrt{13} - 2)p_1 + (5 - \sqrt{13})r_1]/\sqrt{13}.$$

$$66) \quad K_2 = 2[(\sqrt{13} + 2)p_1 - (5 + \sqrt{13})r_1]/\sqrt{13}.$$

$$67) \quad K_3 = [2(1 + v_1 - o_1) - p_1]/4.$$

Examination of the first matings shows that

$$68) \quad o_1 = \frac{r^2}{(r+s)K}; \quad p_1 = \frac{2rs}{(r+s)K}; \quad r_1 = \frac{s^2}{(r+s)K}; \quad v_1 = \frac{t}{K},$$

in which $K = r + s + t$.

Substituting these values into equations 65), 66), 67), we have,

$$69) \quad K_1 = 2s[2r(\sqrt{13} - 2) + s(5 - \sqrt{13})]/[\sqrt{13} \cdot K(r+s)].$$

$$70) \quad K_2 = 2s[2r(\sqrt{13} + 2) - s(\sqrt{13} + 5)]/[\sqrt{13} \cdot K(r+s)].$$

$$71) \quad K_3 = (2t + s)/2K.$$

The expressions for AA , Aa , aa , in terms of r , s , t , are far from neat.

The one for Aa will be given; those for AA and aa can be readily calculated from the one for Aa by using equations 62), 63), 64).

$$72) \quad Aa = \frac{s}{2K \sqrt{13} \cdot 12^n (r+s)} [(5 + \sqrt{13})^n \{ (7 + \sqrt{13})r + (1 + \sqrt{13})s \} + (5 - \sqrt{13})^n \{ (-7 + \sqrt{13})r - (1 - \sqrt{13})s \}].$$

It is instructive to note that

$$\lim_{n \rightarrow \infty} \frac{P_n}{12^{n+c}} = 0.$$

This follows from the fact that $(5 + \sqrt{13})/12$ and $(5 - \sqrt{13})/12$ are proper fractions, and that a proper fraction raised to higher and higher powers approaches zero as a limit. With this in mind we see at once from equation 63) that the proportion of heterozygotes approaches zero as n increases. Then

$$\lim_{n \rightarrow \infty} (AA)_n = 1 - K_s = \frac{2r + s}{2K}, \text{ and}$$

$$\lim_{n \rightarrow \infty} (aa)_n = K_s = \frac{2t + s}{2K}.$$

Here again we see what has been true of every problem in inbreeding, that the heterozygotes tend to disappear and the homozygotes approach the proportion

$$AA/aa = (2r + s)/(2t + s).$$

This is to be expected. In fact the following statement of the case seems obvious:

Any method of breeding which gives A and a gametes equal chances of mating and which tends to eliminate heterozygous individuals will in successive generations give populations which approach a stable condition in which the two types of homozygous individuals appear in the same proportion as were their types of gametes in the original population.

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STUDIES ON SELF-STERILITY I. THE BEHAVIOR OF SELF-STERILE PLANTS

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INTRODUCTION

The occurrence of self-sterility

Among both hermaphroditic animals and plants forms are known in which fertilization of the eggs by sperm or by pollen of the same individual is difficult or even impossible. This condition is known as self-sterility,¹ although the term is not a happy one, since both the male and the female gametes are morphologically perfect and are functional with the complemental gametes of other individuals.

Self-sterility is probably a widespread phenomenon though its presence has been proved experimentally in comparatively few plants and in only one animal. The result, one might even say the aim, of self-sterility, however, is cross-fertilization. Regarded from this standpoint, it is to be classed with the various other specializations of animals and plants, such as morphological differences in the accessory sexual organs, dichogamy, monœcism, dioecism, etc., which tend toward the same end; and since these obvious contrivances for cross-fertilization are so numerous and so disspread, it is difficult to believe that the less easily detected self-sterility is rare, particularly as it has arisen independently in widely separated groups.

The important rôle played by cross-fertilization in the evolution of animals and plants may be attributed in some degree, therefore, to the phenomenon of self-sterility; hence, any light thrown upon its meaning is a contribution toward an explanation of the significance of cross-fertilization in general.

Among animals only *Ciona intestinalis* has been proved to be self-sterile (CASTLE 1896), though the condition is suspected in several other forms.

Among Angiosperms self-sterility is rather generally distributed. KNUTH (1898, Vol. I, pp. 42-45) gives a list of 134 self-sterile species representing 46 families and including both monocotyledons and dicotyledons. This list is the best compilation of recorded cases and may be considered fairly complete to-day as very few additional records have

¹ The words self-incompatibility and self-impotence have been substituted for self-sterility by various writers. These terms seem to us to be neither more nor less objectionable than self-sterility, since neither takes into consideration the fact that the same type of infertility may exist between different individuals. The important point in the matter is that one should not confuse the phenomenon with any of those types of true sterility where there is either complete or partial incapacity for the production of gametes functional *per se*. For a discussion of the differences between self-sterility and true sterility see KRAUS (1915) and SROUT (1916).

appeared in subsequent publications. It is naturally somewhat inaccurate, inasmuch as several cases are recorded in which cross-pollination was merely prevented by bagging the inflorescence or by isolating the plants and self-pollination not insured. Nevertheless, at least 70 percent of the records are properly proved cases of a self-sterility that is something more than an ephemeral condition due to environmental changes or to a fleeting period of reproductive inactivity that is normal in the life history of so many plants.

There remain, then, in the neighborhood of 100 well endorsed instances of self-sterility scattered over some 35 families. These families are so different in their modes of reproduction that no general conclusion can be drawn regarding the development of self-sterility. There are legumes which are usually self-fertilized, and orchids that have developed quite wonderful floral mechanisms favoring cross-fertilization; there are showy flowers, and flowers peculiarly inconspicuous; there are flowers with perfume, and flowers without it; there are anemophilous plants, and plants that would be classed as strictly entomophilous. In certain genera, such as *Passiflora*, there is a general tendency toward self-sterility; in other genera, for example *Verbascum* and *Nicotiana*, closely related species behave very differently.

In other words self-sterility has arisen many times, and often in groups where there was apparently no need for it if the necessity is assumed to be that of cross-fertilization. Not only is this an irresistible argument in favor of the idea already expressed that only a small fraction of the cases of self-sterility have been discovered and that self-sterility has been a much more important factor in plant evolution than has previously been suspected, but it also indicates that certain of the mechanical devices that have received great credit for promoting cross-fertilization were inadequate for the needs of many plants.

EARLY WORK ON SELF-STERILITY

The discovery of self-sterility in plants probably should be credited to KÖLREUTER, the first² real student of hybridization, although his case is somewhat doubtful. KÖLREUTER (1764) found that during two years three plants of *Verbascum phaniceum* set no seed with their own apparently good pollen, although they seeded readily with pollen of *V. Blat-*

²THEOS. FAIRCHILD crossed *Dianthus caryophyllus* with *D. barbatus* in 1719, and LINNEUS brought his hybrid between *Tragopogon pratensis* and *T. porrifolius* into flower in 1759, but neither of them contributed to the world any important facts regarding hybridization.

taria, *V. nigrum*, *V. phlomoides* and *V. Lychnitis*. Later these plants showed sporadic fertility alternating with sterility of pollen or of eggs or of both sex-cells, so that this instance may be only one of induced true sterility due to conditions. It seems to deserve priority as an instance of self-sterility, however, for DARWIN (1872, p. 341) found *V. phæniceum* and *V. nigrum* to be self-sterile, although the related species *V. Thapsus* and *V. Lychnitis* were self-fertile.

SPRENGEL (1793), the other important hybridist of the 18th century does not mention the subject.

Several true instances of self-sterility were discovered by HERBERT (1837) in his experiments with the Amaryllidaceæ. He says:

"Nine very fine crosses of *Hippeastrum* were flowering [there] at the same time; one a natural seedling from *Johnsoni* or *Regio-vittatum*, two, *Johnsoni-pulverulentum*, one *Johnsoni-vittatum*, one *psittacino-Johnsoni* crossed again by *vittato-Johnsoni*, one from *Johnsoni* by *solandriflorum*, and two from *vittato-Johnsoni* by the same. Being desirous of blending again these plants which were all cross-bred, different flowers were touched with pollen from their several neighbors and ticketed, and other flowers were touched with their own pollen. Almost every flower that was touched with pollen from another cross produced seed abundantly, and those which were touched with their own either failed entirely or formed slowly a pod of inferior size with fewer seeds, the cross impregnation decidedly taking the lead."

"It is only from the superior efficacy of the pollen of another plant that we can account for the circumstances of some hybrid plants, which breed freely with plants of either parental stock and fecundate them, not producing seed readily when left to themselves; for if their pollen is able to fertilize and their ovary to be fertilized, there can be no positive sterility in the plant, though there may be a want of sufficient energy under certain, or perhaps under ordinary, circumstances."

These observations of HERBERT referred to hybrids, though he also found self-sterility in the species *Zephyranthes carinata*, and DARWIN in discussing them very properly sets them apart from the cases of self-sterility in pure species. We shall show later, however, that absolute self-sterility exists both in pure species and in hybrids, and is one and the same phenomenon. In fact HERBERT himself very nearly demonstrated this. In a letter to DARWIN (1875) written in 1839, he states that after a duplication of these experiments with like results, he was led to make similar trials on a pure species. He selected a plant of *Hippeastrum aulicum* which he had recently imported from Brazil. Three of its flowers he selfed without result; a fourth flower he crossed with pollen of a triple cross between *H. bulbulosum*,⁸ *reginæ* and *vittatum* and obtained good seed.

⁸ Probably *H. rutilum* Herb.

Later work cited by DARWIN (1875) also supports this idea. BIDWELL in New South Wales found *Amaryllis belladonna* to be partially self-sterile, though fertile to the pollen of other species. E. BERNET, of Antibes, a man having a wide experience in crossing species of *Cistus*, found that their hybrids when fertile (he does not mention the pure species) were completely self-impotent. His statement is that, quoting Darwin, "the flowers are always sterile when the pistil is fertilised by pollen taken from the same flower or from flowers on the same plant." "But," he says—without the italics—"they are often fertile if pollen be employed from a distinct individual of the same hybrid nature, or from a hybrid made by a reciprocal cross." A. RAWSON, a well known English horticulturist, found the same absolute self-sterility in various named varieties of *Gladiolus* that were said to have descended from *Gandavensis*, an old race produced by crossing *G. natalensis* by *G. oppositiflorus*. The interesting point in RAWSON's work was that none of the plants of the same variety would set seed when interpollinated. As each variety had been propagated asexually by bulbs, he was of course actually dealing with plants of the same germinal constitution, though under somewhat different environmental conditions. For this reason it is extremely improbable that these were cases of induced true sterility.

"Altogether, Mr. RAWSON, in the year 1861 fertilised twenty-six flowers borne by four varieties with pollen taken from other varieties, and every single flower produced a fine seed capsule; whereas fifty-two flowers on the same plants, fertilised at the same time with their own pollen [which had been proved to be good by the crosses], did not yield a single seed capsule."

Returning to the phenomenon as exhibited in pure species, WM. MOWBRAY, gardener of the Earl of Mountnorris, in a letter to the Secretary of the HORTICULTURAL SOCIETY (England), dated October 29, 1830, states that he could get fruit only from *Passiflora alata* and *P. racemosa* by reciprocal fertilization.

Observations on self-sterility in this genus continued to be made later by a number of observers. The most important work was done by ROBERTSON MUNRO (1868). MUNRO found *P. alata*, *P. racemosa*, *P. carulea*, *P. Bellottii*, *P. kermesina*, *P. holosericea* and *P. fulgens* to be self-sterile, while DARWIN obtained evidence that *P. laurifolia* and *P. quadrangularis* were in the same condition. The evidence of perfect self-sterility in the first three species is incontrovertible, in the remaining species it is highly probable.

Some of the details from MUNRO's work are exceedingly interesting.

In the first place he found plants of *P. alata* to be highly fertile with their own progeny as the following quotation shows.

"I impregnated a considerable number of these flowers with their own pollen, everyone of which proved abortive. But on impregnating eighteen flowers on the mother plant with pollen from her own self-impotent seedlings, I got eighteen fine plump ovaries full of seed."

Again, MUNRO found that self-sterile plants were sometimes cross-fertile and sometimes cross-sterile with plants of the same species and presumably of the same generation. For example, three self-sterile plants of *P. carulea* all produced seeds with pollen from one other plant. The same experiment on *P. alata* showed cross-sterility in two instances and cross-fertility in one instance.

A curious case of a return to self-fertility in *P. alata* through grafting was also reported by MUNRO. Mr. DONALDSON, gardener at Keith Hall, grafted a self-sterile plant upon stock of an unknown species. Though its pollen still refused to fertilize certain other plants of the same species, it was markedly self-fertile and fertile with at least one other plant. Seedlings from this plant were all self-sterile but were fertile with the mother plant.⁴

GÄRTNER (1849), who was among the most reliable of the early hybridizers, found a number of self-sterile species. *Dianthus japonicus* was sterile both with its own pollen and with the pollen of *D. barbatus*. Two plants of *Lobelia fulgens* likewise proved self-sterile. Their pollen was good on *L. cardinalis* and *L. syphilitica*, their ovules could be fertilized by the pollen of these species, but self-pollination yielded nothing. A plant of *Verbascum nigrum* was also completely self-impotent though fertile as a male with *V. Lychnitis* and *V. austriacum* and fertile as a female with *V. Thapsus*.

Similar conditions in certain exotic orchids were reported by SCOTT (abstract 1863, complete paper 1865). A duplicate of a table in his paper and a summary of his conclusions follow.

SCOTT and MUNRO (DARWIN 1875) each independently found *Oncidium sphacelatum* also to be wholly self-sterile after some three hundred attempts at self-pollination, though the species was fertile reciprocally with other *Oncidiums*. MUNRO in addition confirmed SCOTT's observations on *O. divaricatum* and added *O. flexuosum* to the list of self-sterile plants.

⁴ It is likely that this phenomenon is similar to the pseudo self-fertility due to conditions, which is discussed later in this paper.

Unions between *Oncidium microchilum*, *O. divaricatum* var. *cupreum* and *O. ornithorhynchum*.

	Number of flowers fertilized	Total number of capsules produced	Number of good capsules	Estimated number of seeds	Estimated number of good seeds	By calculation	
						Total seeds	Good seeds
1. <i>O. ornith.</i> × <i>O. micro.</i> (No. 2)	8	3	3	20200	4242	or as 1000 to 210	
2. <i>O. micro.</i> (No. 2) × <i>O. ornith.</i>	12	0					
3. <i>O. ornith.</i> × <i>O. micro.</i> (No. 1)	8	5	4	23360	3737	or as 1000 to 160	
4. <i>O. micro.</i> (No. 1) × <i>O. ornith.</i>	12	2	0				
5. <i>O. divar. cup.</i> × <i>O. micro.</i> (No. 2)	6	3	3	22050	7938	or as 1000 to 360	
6. <i>O. micro.</i> (No. 2) × <i>O. divar. cup.</i>	18	2	0				
7. <i>O. divar. cup.</i> × <i>O. micro.</i> (No. 1)	6	4	4	26240	8922	or as 1000 to 340	
8. <i>O. micro.</i> (No. 1) × <i>O. divar. cup.</i>	6	2	2	17700	1434	or as 1000 to 420	
9. <i>O. micro.</i> (No. 1) × <i>O. micro.</i> (No. 2)	6	5	4	45800	34350	or as 1000 to 750	
10. <i>O. micro.</i> (No. 2) × <i>O. micro.</i> (No. 1)	18	0					
11. <i>O. micro.</i> (No. 1) × own pollen	24	1					
12. <i>O. micro.</i> (No. 2) × own pollen	24	0					

"By a summary comparison of these results we have the following highly interesting facts disclosed. First, we see that the male element of *O. microchilum* (No. 1) will fertilise the female element of the two distinct species *O. ornithorhynchum* and *O. divaricatum* var. *cupreum* and yet be completely impotent upon its own female element; nevertheless the susceptibility of the latter (female element) to fertilisation is shown by its fertile unions with another individual of the same species, and likewise by a fertile union with an individual of a distinct species, namely *O. divaricatum* var. *cupreum*. Secondly, the male element of *O. microchilum* (No. 2) will fertilise the female element of *O. ornithorhynchum* and *O. divaricatum* var. *cupreum*, and likewise another individual of its own species, though on its own female element it is utterly ineffective."

These observations, together with similar ones on *O. Cavendishianum* recorded by LECOQ (1862) from the experiences of RIVIÈRE were made on hot-house plants and DARWIN originally attributed their self-sterility to the peculiar conditions under which they were grown. He was forced to modify his conclusions, however, through information received from FRITZ MÜLLER. The latter self-fertilized over one hundred flowers of *Oncidium flexuosum* at Desterro, Brazil, where it is native, without obtaining a single seed, but he did discover the important fact⁵ that each plant *was fertile with the pollen from any other plant*.

SCOTT and MÜLLER each independently made the further discovery that the tissue of the style of the self-sterile plants was penetrated freely by the pollen tubes after selfing, though fertilization did not subsequently occur.

As DARWIN noted:

"Another observation made by FRITZ MÜLLER is highly remarkable, namely that with various orchids the plant's own pollen not only fails to impregnate the flower, but acts on the stigma, and is acted on, in an injurious or poisonous manner."

We have not been able to find any confirmation of these results, and it seems entirely probable that the apparently poisonous action of the pollen after an "illegitimate" pollination, might have been due to the action of bacteria or fungi, since the work was done under tropical conditions. But the facts are so exceptional that we give DARWIN'S (1875, vol. 2, p. 112) account.

"FRITZ MÜLLER observed the poisonous action of the plant's own pollen in the above mentioned *Oncidium flexuosum*, *O. unicorn*, *pubes* (?), and in two unnamed species. Also in two species of *Rodriguezia*, in two of *Notylia*, in one of *Burlingtonia*, and of a fourth genus in the same group. In all these cases, except the last, it was proved that the flowers were, as might have been expected, fertile with the pollen from a distinct plant of the same species. Numerous flowers of one species of *Notylia* were fertilised with pollen from the same raceme; in two day's time they all withered, the germens began to shrink, the pollen masses became dark brown, and not one pollen grain emitted a tube. So that in this orchid the injurious action of the plant's own pollen is more rapid than with *Oncidium flexuosum*. Eight other flowers on the same raceme were fertilised with pollen from a distinct plant of the same species; two of these were dissected and their stigmas were found to be penetrated with numberless pollen tubes; and the germens of the other six flowers became well developed. On a subsequent occasion many other flowers were fertilised with their own pollen, and all fell off dead in a few days; whilst some flowers on the same raceme which had been left simply unfertilised adhered and long remained fresh. We

⁵ It is probable that cross-sterility existed, but was not discovered.

have seen that in cross unions between extremely distinct orchids the pollen long remains undecayed; but *Notylia* behaved in this respect differently; for when its pollen was placed on the stigma of *Oncidium flexuosum*, both the stigma and pollen quickly became dark brown, in the same manner as if the plant's own pollen had been applied."

MÜLLER suggests an explanation of this phenomenon which must be pleasing to the minds of strict Natural Selectionists. He believes it to be an advantage to the species to have its pollen positively deleterious rather than simply neutral, because the flowers would then soon drop off, and the energies of plants no longer be directed toward nourishing a part which would not finally function.

Another quotation from DARWIN (*ibid.*, p. 113) is interesting both for the facts contained and for the deductions of MÜLLER.

"The same naturalist found in Brazil three plants of a *Bignonia* growing near together. He fertilised twenty-nine flowerets on one of them with their own pollen, and they did not set a single capsule. Thirty flowers were then fertilised with pollen from a distinct plant, one of the three, and they yielded only two capsules. Lastly, five flowers were fertilised with pollen from a fourth plant growing at a distance, and all five produced capsules. FRITZ MÜLLER thinks that the three plants which grew near one another were probably seedlings from the same parent and that from being so closely related, they acted very feebly on one another. This view is extremely probable for he has since shown in a remarkable paper (MÜLLER 1873) that in some Brazilian species of *Abutilon*, which are self-sterile, and between which he has raised some complex hybrids, that these, if near relatives were much less fertile *inter se*, than when not closely related."

This work of MÜLLER (1873) consisted in noting the fertility of various matings of 8 species of *Abutilon* that he denotes by the letters A, C, E, F, M, P, S and V, the individual plants being distinguished by subscripts. Thus the plants $EF.F_1$ and $EF.F_2$ are similar combinations formed by crossing species E with species F and crossing the first generation hybrids thus formed with F_1 and F_2 . The principal results were as follows:

Number of flowers	Mother plant	Source of pollen	Number of fruits	Average No. of seeds
9	$F.EF_1$	Others of same stock		
20	$F.EF_1$	$F.EF_1$, $EF.F_1$ and $EF.F_2$	3	1.3
10	$F.EF$	FE and FE_2	10	4.5
11	$F.EF$	EF_2 and EF_3	10	4.6
10	$F.EF$	F_1	9	4.6
6	$F.EF$	$F.CF_1$ and $F.CF_2$	6	4.5
1	$F.EF$	FS_1	1	4.7

He says that the results following the intercrossing of sister plants

were not due to bad pollen, as on other plants it was completely potent; the pollen of $F.EF_2$ producing fruit full of seeds on FS_1 , that of $EF.F$ on FE_2 , that of $EF.F_2$ on F , and that of $F.EF_1$ on F , $F.CF_2$, FS_1 and FS_2 . In explaining the phenomenon he follows DARWIN in supposing inbreeding to be the cause.

Most of these observations and investigations were known to DARWIN who not only published historical accounts in the "Origin of species" and "Variation of plants and animals under domestication," but between 1860 and 1880 carried out numerous experiments on the subject which were reported in a series of papers in the JOURNAL OF THE LINNEAN SOCIETY and other places and were brought together in the three classics, "On the various contrivances by which British and foreign orchids are fertilised by insects" (1862), "The effects of cross- and self-fertilisation in the vegetable kingdom" (1876), and the "Different forms of flowers on plants of the same species" (1877).

DARWIN'S investigations on fertilization in the orchids are only remotely related to the subject in hand, but his experiments on heterostyled dimorphic forms are, we believe, concerned with an analogous phenomenon. The "illegitimate" unions according to DARWIN include certain matings other than self-pollination, but the greatly decreased fertility after self-pollination in practically all of these species as well as the absolute self-sterility of so many forms indicate that the condition is one like ordinary self-sterility though complicated by a linkage with style length and with pollen size. The work of BATESON and GREGORY (1905) on the inheritance of heterostylism in *Primula* has done something toward clearing up these relationships, but much remains for the future. As these investigations of DARWIN are readily available and cannot, at present, add materially to our discussion of self-sterility on account of moot points, they will not be described further; but we shall abstract from the experiments on those plants usually considered to be genuinely self-sterile.

DARWIN (1876) investigated rather thoroughly the conditions in five self-sterile species, *Eschscholtzia californica*, *Abutilon Darwinii*, *Senecio cruentus*, *Reseda odorata* and *R. lutea*.

A plant of *Eschscholtzia californica* had been accidentally found to be self-sterile by FRITZ MÜLLER (1868, 1869) while working in southern Brazil. This induced him to investigate its behavior through six generations, during which time he found all of the plants to be completely self-sterile though fertile between themselves. As DARWIN had found

English plants comparatively self-fertile and as HILDEBRAND had discovered no complete self-sterility in plants grown in Germany, he obtained from MÜLLER seed of the Brazilian plants known to be self-sterile and from them raised seedlings. These while not wholly self-fertile, tended toward fertility, which fact DARWIN attributed to the lower English temperature. A second generation of seedlings proved to be still more self-fertile. Conversely, seed of English stock sent to Brazil proved to be more self-fertile than the native race, though one plant thus exposed to the climate of Brazil for two seasons, was wholly self-sterile.

These results were paralleled by the behavior of *Abutilon Darwinii* which is self-sterile in its native Brazil, but became moderately self-fertile *late in the first flowering season* in DARWIN's greenhouse.⁶

DARWIN made no extensive experiments on self-sterility with Brazilian plants in collaboration, so to speak, with FRITZ MÜLLER; but this was not for the lack of material, for in a letter to FOCKE (1893), MÜLLER says the number of self-sterile species of plants in Brazil is very large, and that different species of the same genus often behave differently in regard to self-pollination. He observes that self-sterility is often associated with unusual vegetative vigor and that species of *Oxalis* having trimorphic flowers which are all self-sterile make unusually vigorous growths. This condition observed by MÜLLER is doubtless merely another example of the hybrid vigor or heterosis so common among both plants and animals, and shows the reason, of course, why self-sterility has been maintained by natural selection.

DARWIN's experiments on *Senecio cruentus* are noteworthy only because the varieties used were descendants of garden hybrids.

Two plants of a purple-flowered and one plant of a red-flowered variety were found to be self-sterile and cross-fertile.

The experiments with *Reseda odorata* were more detailed. Those of 1868 are shown in tabular form, the letters representing individuals and the subscripts pollinations. As may be seen, the seven plants used were absolutely self-sterile. The number of pollinations made allow us no doubts about the matter, F and G being selfed many times as well as the others, though in these two cases no figures were reported. Sixteen cross-matings, on the other hand, were all fertile.

In the spring of 1869, four other plants were raised from fresh seed and isolated under nets. Three of these proved to be wholly self-fertile, while the fourth was not completely self-sterile.

⁶ Cf. our results on flowers late in the season.

DARWIN's experiments on *Reseda odorata* in 1868.

		Male parents					
		A	B	C	D	E	F
Female parents	A	S ₁₆	F	F			
	B	F	S ₁₈	F	F		
	C	F	F	S ₁₉	F	F	
	D	F	F	F	S ₁₈	F	
	E	F		F	F	S ₈	
	F						S
	G						S

Much surprised at these divergent results DARWIN raised six more plants in 1870. Of these, two were almost self-sterile and four were completely self-fertile. The former produced altogether five seeds, which were grown the following year. These plants made a luxuriant growth, but were almost completely self-sterile like their parents [an indication of pseudo-fertility]. The progeny of the self-fertile plants was not followed.

These varying results were attributed by DARWIN to a difference in inherited sexual constitution. He says in his general conclusions (1876, p. 346):

"Finally, the most interesting point in regard to self-sterile plants is the evidence which they afford of the advantage, or rather of the necessity, of some degree or kind of differentiation in the sexual elements, in order that they should unite and give birth to a new being. It was ascertained that the five plants of *Reseda odorata* which were selected by chance, could be perfectly fertilised by pollen taken from any one of them, but not by their own pollen; and a few additional trials were made with some other individuals, which I have not thought worth recording. So again, HILDEBRAND and FRITZ MÜLLER frequently speak of self-sterile plants being fertile with the pollen of any other individual; and if there had been any exceptions to the rule, these could hardly have escaped their observation and my own. We may therefore confidently assert that a self-sterile plant can be fertilised by the pollen of any one out of a thousand or ten thousand individuals of the same species, but not by its own. Now it is obviously impossible that the

sexual organs and elements of every individual can have been specialised with respect to every other individual. But there is no difficulty in believing that the sexual elements of each differ slightly in the same diversified manner as do their external characters; and it has often been remarked that no two individuals are absolutely alike. Therefore we can hardly avoid the conclusion, that differences of an analogous and indefinite nature in the reproductive system are sufficient to excite the mutual action of the sexual elements and that unless there be such differentiation fertility fails."

These inductions are cleverly drawn and clearly expressed, but they are not all justified by the data in DARWIN'S possession. The matings between self-sterile plants made by HILDEBRAND, MÜLLER and DARWIN were neither individually nor collectively sufficient to establish the point that "a self-sterile plant can be fertilized by the pollen of any one out of a thousand or ten thousand individuals of the same species," and it is upon this supposition that the generalization is based. Further, MUNRO, whose work was known to DARWIN, had found cross-sterility in *Passiflora*.

As it is not proposed to make this review a check list of species which are, as a whole or in part, self-sterile, but rather to set forth the known facts concerning the behavior of self-sterile plants and to outline the various theories that have been suggested to interpret the phenomenon, we shall pass DARWIN'S conclusions without further comment. His work properly stands as the outpost of advance in the subject until the re-discovery of Mendel's Law in 1900. The method of analysis of pedigree cultures foreshadowed by VILMORIN but really initiated by MENDEL has made a methodological revolution. It seems fitting, however, to close this part of our paper with the work of a botanist who, though making no outstanding contributions to the subject, was a contemporary of and an aid to DARWIN, and who from the chronological standpoint links the work of DARWIN to that of the present day.

HILDEBRAND worked and wrote indefatigably upon questions of fecundation in plants from 1863 until 1908. His first paper (1863), on dimorphism in *Primula sinensis* appeared almost simultaneously with that of DARWIN, and since that time in the neighborhood of seventy contributions on similar subjects have appeared under his name.

HILDEBRAND (1866) published some rather extensive experiments with *Corydalis cava* in which he showed that the plants were absolutely self-sterile although both pollen and ovules were functional. But his investigations were noteworthy with respect to the large number of species in which he established a high probability of self-sterility, rather

than for any fundamental researches on the genetic problem concerned. We will mention only one other paper, therefore, merely to show the large numbers of self-sterile plants that are sometimes (possibly often) to be found in a single family when said family is even partially investigated.

In 1896 he published on the Cruciferæ and found *Hesperis tristis*, *Lobularia maritima* (= *Alyssum maritimum* Lam.), *Cardamine pratensis*, *Rapistrum rugosum*, *Iberis pinnata* and *Sobolewsia clavata* fully self-sterile, *Aethionema grandiflorum* and *Hugueninia tanacetifolia* (= *Nasturtium tanacetifolium* Hook.) nearly self-sterile, and only *Draba verna* and *Brassica rapa* fully self-fertile.

RECENT WORK ON SELF-STERILITY

The work of the last decade on self-sterility has been less concerned with the discovery of new cases than with an interpretation of the phenomenon in keeping with modern biological thought. Several noteworthy investigations on both plants and animals have appeared.

JOST (1907) repeated HILDEBRAND'S experiments on *Corydalis cava*, and unlike the latter, observed a small percentage of self-fertility. In his experiments 93 selfed plants yielded 6 capsules, whereas 42 crossed plants produced 30 capsules. Self-sterility was also noted in *Secale cereale* (a variety *montanum*) and *Lilium bulbiferum*. The immediate cause of the different behavior of these plants after self-pollination and after cross-pollination was found to be the difference in rate of pollen-tube growth. In *Secale*, pollen tubes were found to have penetrated the micropyle in about eight hours after cross-pollination, although after self-pollination the tubes had merely reached the base of the pistil after twenty-four hours. Pollen tubes also appeared to grow somewhat faster than after self-pollination when crosses (?) were made between flowers on the same plant, but in view of the fact that asexually propagated plants from a single seed appear to behave very similarly this observation may not be correct. In this connection it should be mentioned that FOCKE (1890 and 1893) found that *Lilium bulbiferum* plants of the same clonal variety were completely cross-sterile, although sister seedlings were cross-fertile. Similar observations on asexually propagated pome fruits have been made by WAITE (1895) and LEWIS and VINCENT (1909), but in these cases "fruitfulness" rather than "fertility" was noted.

To explain his results JOST had recourse to the old concept of "Individualstoffe." He believes that individuals not only of the same species

but of the same family differ qualitatively in their chemical composition, that the gametes of any plant possess the "Individualstoff" of that plant, and that pollen tubes grow well only in tissues having a different "Individualstoff."

In 1912 a very important paper by CORRENS appeared in which a Mendelian interpretation of results was proposed. His experimental work began with a hybrid between *Petunia nyctaginiflora* and *Petunia violacea* that had been produced in 1901, and of which 11 individuals had passed through the winter. Six of these plants were found to be self-fertile, three completely self-sterile and two nearly self-sterile. Among the self-sterile plants certain combinations proved easy to make, while others were impossible. It was sometimes impossible even to cross the self-sterile with the self-fertile plants [probably pseudo-fertile]. For several reasons, however, CORRENS found *Petunia* unsatisfactory and the work was dropped until 1910; it was then recommenced with *Cardamine pratensis*, a Crucifer that had been shown to be wholly self-sterile by HILDEBRAND (1896).

Concerning the "cause" of self-sterility, borrowing the term from the author, he gives the following facts: The pollen grains germinated on the stigma of the self-pollinated flowers, but produced only short tubes that did not penetrate the tissues of the stigmas, while after cross-pollination the pollen tubes were found in the upper part of the ovaries after only 48 hours.

The pedigree culture investigations began with two plants, B having very light lilac flowers, and G having flowers of a more intense lilac. These plants were crossed reciprocally, the combination $B^{\text{♀}} \times G^{\text{♂}}$ being designated No. 1 and the other No. 2. From each of these matings, 30 plants were raised, and formed the basis of the remaining experiments. They were numbered 1a, 1b, 1c, - - - 2a, 2b, 2c, etc.

These plants were first tested for their fertility when used as females by crossing each individual with the pollen of two unrelated plants from Lake Zürich and Schwabia respectively. These pollinations were successful without an exception, proving that pollen from a single plant could fertilize each of the 60 F_1 sibs.

From 3 to 15 pollinations were then made upon every F_1 plant with the pollen of each parent B and G. About half of these pollinations were uniformly fruitful or uniformly unfruitful as the case might be, but the other half showed variations in behavior that made classification of the results difficult. For example out of ten pollinations of plant 10

with the pollen of B, 6 were successful and 4 unsuccessful. This plant was classed as fertile with B. Again, plant 1k pollinated 7 times with the pollen of G yielded 3 good capsules, 2 poor capsules and 2 failures. CORRENS classes this plant as sterile with G with a question mark. These results seem at first sight to indicate a definitely graduated fertility in *Cardamine*. This is not impossible; but, arguing from our own experience (*Nicotiana glauca*), it appears to be more probable that the plant is in a rather unstable condition physiologically and can be influenced easily by external conditions.

CORRENS did endeavor to test the question of the influence of age of plant on fertility by (1) making 17 duplicate pollinations the next year with pollen from a plant raised from a cutting of B, and by (2) making 18 reciprocal pollinations from the F_1 plants upon B and G. The pollinations with pollen from the cutting of B made in 1912 checked with those made in 1911 with pollen from the original plant B in a remarkable manner. Of the reciprocals, 7 were successful both ways, 5 failed both ways, 4 were rather indefinite but similar, while only one showed a conflicting result (2 failures one way and 3 successes the other).

In spite of these facts, however, it is apparent from CORRENS's account that the plants were at all times kept in as fine condition as possible so that the behavior under a poor environment or during different phases of the flowering period was really not determined. What these experiments did do was to prove beyond a reasonable doubt the physiological similarity of cuttings with respect to cross-fertility and cross-sterility, and to indicate that reciprocal crosses always behave in the same manner. Unfortunately for the latter thesis, however, there are a few conflicting results in his table 8, though this he does not mention. Of the 53 reciprocals recorded there, 31 give the same results, 17 give different results, while 5 are questionable.

CORRENS concluded that the behavior of the F_1 individuals with the pollen of the parents was such as to indicate equal-sized classes of definitely fertile or definitely infertile plants, the behavior of the reciprocals being the same. His classification gave the following groups:—fertile with B, 32; sterile with B, 28; fertile with G, 30; and sterile with G, 30.

He further concluded that the action of an F_1 individual toward one parent was wholly independent of its action toward the other, and that the population could be divided into 4 classes with reference to the behavior of the individuals toward both parents, as follows:

Fertile with both B and G, type bg,	16 plants
Fertile with B, sterile with G, type bG,	16 plants
Fertile with G, sterile with B, type Bg,	14 plants
Sterile with both B and G, type BG,	14 plants

An explanation of these facts was sought by assuming that each parent B and G carried at least one transmissible factor, *B* and *G* respectively, which actively inhibited pollen-tube growth, besides at least one inactive factor, *b* and *g* respectively. The formulae for these plants would then be *Bb* and *Gg*, and when they are crossed four equal-sized classes of zygotes will be formed *BG*, *Bg*, *bG* and *bg*, because *B* and *b*, and *G* and *g* segregate at reduction. These four F_1 classes should behave when back-crossed with each parent in the manner shown above.

There seems to be no reason in his hypothesis why plants of the type *bg* should not be self-fertile though this is not the case. In fact all of the 60 F_1 plants are assumed to be self-sterile although two cases showing some self-fertility (probably pseudo-fertility) are shown in table 8c. But this discrepancy is probably due to an imperfect description of the hypothesis by the author, as the relation between self-fertile and self-sterile plants is evidently meant to be left out of consideration.

The intra-class and inter-class pollinations between the F_1 plants of which he made about 700 (tables 8a-8d), hardly come up to expectations, but there is a regularity that cannot be overlooked.

COMPTON (1913 a) confirmed DARWIN's report that both self-fertile and self-sterile plants occur in the mignonette, *Reseda odorata*. From experiments on crossing these two races he obtained the following facts:

(1) Self-sterile plants when bred *inter se* threw self-sterile offspring only. This was thought to indicate that self-sterility is a Mendelian recessive. (2) Certain self-fertile plants, when self-fertilized gave self-fertile offspring only. When crossed with self-sterile plants the same result was obtained. These plants COMPTON regarded as homozygous dominants. (3) Other self-fertile plants, when self-fertilized, gave approximately 3 self-fertile to 1 self-sterile offspring. The same plants crossed with self-sterile individuals produced about one-half self-fertile and one-half self-sterile progeny. These he regarded as heterozygous. All of these facts are satisfactorily interpreted by the hypothesis that self-fertility is a simple dominant to self-sterility.

In a later paper COMPTON (1912) suggests, as JOST had previously done, the presence in the pistil of diffusible substances which stimulate or retard pollen-tube growth after cross- or self-pollination respectively.

The growth of pollen tubes in the style and the growth of fungus hyphae in a host appealed to COMPTON as analogous, and he suggests that self-sterility may be due to agents similar to those which govern immunity or susceptibility in animal or plant.

These results confirm a Mendelian hypothesis already suggested by BAUR (1911) without reporting detailed results. He crossed the self-sterile *Antirrhinum molle* with the self-fertile *A. majus* and obtained only self-fertile offspring. The F_2 generation consisted of both self-fertile and self-sterile plants, the former being in the majority. BAUR gave these hybrids to LOTSY (1913) who raised a large F_2 generation with similar results although he was inclined to believe that the plants showed variable degrees of self-fertility and self-sterility. Neither COMPTON, BAUR nor LOTSY touched the question of the behavior of self-sterile plants among themselves.

Since self-sterility was discovered in the Ascidian *Ciona intestinalis* by CASTLE (1896), its reproductive behavior has been studied by MORGAN (1905, 1910), MORGAN and ADKINS (MORGAN 1913), and FUCHS (1914a). MORGAN and ADKINS showed that these animals vary in degree of self-sterility. Perfectly self-sterile individuals were the exception, but self-fertility never equaled cross-fertility. Individuals also varied in the ease with which their eggs might be fertilized by the sperm of other individuals. The following matings were made with the results noted in percentage of eggs fertilized:

♂	A	B	C	D	E
♀					
A	0	87	92	84	96
B	38	0	35	98	97
C	93	96	0	97	96
D	91	98	77	0	89
E	96	92	60	74	0

FUCHS (1914 a), however, has criticized MORGAN's work, maintaining that 100 percent of segmenting eggs can be obtained in every cross with normal ova if sufficiently concentrated sperm suspension be used. He showed, among other things; that (1) an increased concentration of sperm suspension caused an increase in the number of eggs self-fertilized, (2) a greater concentration of sperm was usually necessary to bring about any self-fertilization than would cross-fertilize 100 percent of foreign eggs, and (3) contact with suspension of own sperm decreased the ease of later cross-fertilization.

The work of FUCHS suggests a physico-chemical basis for self-sterility, since contact of eggs with their own sperm appears to cause changes in the egg membranes which inhibit entrance of own sperm and to some extent of foreign sperm, yet his criticism of MORGAN's statements is not to the point for by the submission of the eggs to different sperm concentrations he has increased the number of variants under investigation.

MORGAN (1913, p. 217) explained his facts by means of this hypothesis:

"This failure to self-fertilize, which is the main problem, would seem to be due to the similarity in the hereditary factors carried by the eggs and sperm; but in the sperm, at least, reduction division has taken place prior to fertilization, and therefore unless each animal was homozygous (which from the nature of the case cannot be assumed possible) the failure to fertilize cannot be due to homozygosity. But both sperm and eggs have developed under the influence of the total or duplex number of hereditary factors; hence they are alike, i.e., their protoplasmic substance has been under the same influences. In this sense, the case is like that of stock that has long been inbred, and has come to have nearly the same hereditary complex. If this similarity decreases the chances of combination between sperm and eggs, we can interpret the results."

This interpretation of self-sterility endeavors to give a modern rendering of DARWIN's idea that the condition is analogous to the decreased fertility often resulting from other modes of inbreeding. From his other numerous observations on cross- and self-fertilization, DARWIN felt instinctively that such an analogy should exist, even though self-sterile plants were continually cross-pollinated and must of necessity have a mixed ancestry. MORGAN's contribution was to show in a general way how such a similarity might come about. His suggestion is unquestionably stimulating and we have been glad to acknowledge our indebtedness to it (EAST 1915).

One should not ascribe more breadth to the hypothesis than the author really intended, however; for certain coördinate problems that may or

may not have the same underlying cause, were not included in its scope. For example, it assumes nothing regarding the origin of self-sterility or the difference between self-sterility and self-fertility. At first sight one feels that there is a great weakness in its failure to account for self-fertility, since the eggs and sperms of self-fertile races also develop under the influence of the total or duplex number of hereditary factors, and it is difficult to see why this should decrease the attraction between eggs and sperm in some cases and not in others. But the *difference* between self-fertile and self-sterile organisms is not of necessity the same problem as the *behavior* of self-sterile organisms.⁷ This distinction is manifest if one refers to COMPTON's work. In his material the difference between self-fertility and self-sterility is that of a single Mendelian factor,—self-sterility being recessive. But COMPTON does not attempt to account for the behavior of his self-sterile plants.

DARWIN, on the other hand, made no serious attempt to interpret the behavior of self-sterile plants, or to describe the fundamental difference between self-fertile and self-sterile races. He was concerned chiefly with the origin of self-sterility. The basic reason for the evolution of self-sterility, he thought, lay in a *necessity* for cross-fertilization. In this we believe he was unwise. The benefits of cross-fertilization, no one doubts. With the vigor of heterozygosis as the immediate advantage for natural selection to grasp, with the immense ultimate advantage of multiplicity of forms brought about by Mendelian recombination, one can see reason in all the host of devices for producing cross-fertilization in animals and plants,—including even bisexuality itself. But this does not mean that cross-fertilization is an inevitable need, as DARWIN believed was so clearly demonstrated by his observations on the deleterious effects of inbreeding. It is rather merely an asset in the struggle for existence, as recent experiments have shown.⁸ Consequently emphasis should be placed on the assured benefits of cross-breeding and not on the doubtful evils of inbreeding. One can understand therefore why self-sterility might be desirable, and why it should be retained by natural selection after coming into existence, but the cause of its origin must still be denoted by that useful word *chance*, the veil of ignorance.

In view of these facts—and all of the important facts regarding self-sterility have been cited—the fundamental questions involved are almost as obscure now as they were when DARWIN left them. But the work of

⁷ STOUT (1916) continually confuses these two problems.

⁸ See EAST and HAYES (1912) and the papers there cited.

MORGAN, CORRENS and COMPTON encourages the hope that their solution, if one may use that term for scientific description, will be accomplished. An interpretation in harmony with modern biological conceptions which will in its turn be helpful, ought at least to be possible when all of the facts are at hand.

Since the historical part of this paper was written, STOUT (1916) has published a bulky memoir on self-sterility in *Cichorium intybus*. A large portion of this paper is devoted to destructive criticism. DARWIN and his contemporaries, BAUR, COMPTON, CORRENS, EAST, JOST, LOTSY, MORGAN and SHULL are "placed upon the carpet" and dealt with severely. One wonders whether all of these writers can be wholly wrong in the views that have been assailed, and if not, just wherein the differences of opinion lie. We cannot help but feel that they are due largely to his misconceptions of the views of the various writers concerned.

As examples of what is meant by this statement, let us mention two of the points on which STOUT lays great stress. He feels strongly that self-sterility is a markedly variable character, and that this has not been recognized by previous writers. But since the existence of variability in the somatic expression of self-sterility has been admitted unanimously by the writers with whom we are acquainted, the true point at issue is not this, but rather the question whether any considerable part of the variation in this character is the result of genetic differences. This question has been investigated in *Nicotiana*, and there the variation seems to be almost wholly due to environmental changes, as is shown later in this paper. Considered with this point in mind, a reasonable and constructive interpretation of our own and many other self-sterility data can be given. Where before there was chaos a certain order appears. STOUT's failure to recognize these truths is probably the reason why he has been unable to make any constructive analysis of his own numerous data for the fact that some of his families arising from selfed seed behaved exactly as the families arising from crossed seed shows that he is often (at least) dealing with a pseudo self-fertility (see p. 531).

Now this argument of STOUT's, we gather, is meant to be only a particular instance advanced in favor of his general view that characters are (always?) too variable genetically to be represented properly by fixed Mendelian factors. The justice or injustice of such a contention cannot be discussed here, but we should like to point out that in assuming—as is so often done—that geneticists commonly believe in an ele-

mental stability of characters, the attitude of the great majority of such workers is misconstrued. If we have interpreted Mendelian investigators' views correctly, they believe that characters are variable, but in different degrees in different species; and that there is adequate evidence to show that most characters in most species are so constant throughout the number of successive generations ordinarily available for experimental purposes when viewed under the conditions most likely to eliminate variables other than heredity, that the *abstract* idea of fixed germinal factors can be used properly and helpfully in genetic analysis.

As a second case where we believe STOUT has not represented fairly the views of the writers criticized, the section of his paper entitled "Relation of vegetative vigor and fertility to inbreeding and cross-breeding" may be cited. STOUT criticizes in particular the views of DARWIN, SHULL, and EAST and HAYES on this subject. He rests his case on a paper by BURCK (1908) in which the writer holds, that (quoting STOUT):

"(1) plants that are regularly self-fertilized show no benefits from crossing, (2) that nowhere in wild species is there evidence of an injurious effect from self-fertilization, and that there is abundant evidence of continued vigor and high fertility resulting from long-continued self-fertilization, and (3) that the advantage derived from crossing within or between garden varieties appears when there is doubtful purity; and is due to the fact that both vigor and fertility have already been decreased by hybridization, and that when crosses do give increased vigor and fertility the cross has restored in increased measure the original nuclear organization of the parent species."

The logic of the third statement is too delightful for comment, being worthy indeed of Mother Eddy. Vigor is decreased by hybridization. Vigor is increased by hybridization. It is increased by restoring "nuclear organization." Not only is nuclear organization restored, but it is restored in "*increased measure*."

The second statement has never been denied by modern writers, to our knowledge. It was emphasized by EAST and HAYES (1912), who pointed out why the advantage of cross-fertilization in plants should be stressed rather than the disadvantage of self-fertilization. This advantage, if one may recall it, lies in the fact that n inherited variations can produce but n forms under self-fertilization, and may produce 2^n forms under cross-fertilization by Mendelian recombination.

The first statement is simply not in accord with the facts. We are astonished that one who has the acquaintance with the literature that

STOUT has shown, should quote it with approval. Every hybridist of experience from KÖLREUTER (1760) to the present day has cited so many data diametrically opposed to it that the matter is no more worthy of discussion than is a denial that the earth is round.

Of course as to the interpretation of the facts one may hold a difference of opinion. The hypothesis of heterosis advanced independently by SHULL and EAST has, we think, served a useful purpose. The last word has not been said, however, and data accumulated by H. K. HAYES and D. F. JONES in their continuation of the experiments reported by EAST and HAYES (1912) have led the senior author to modify his views on several of the points there discussed, though not on the main conclusions. But in the meantime it is disconcerting to have our published statements misunderstood and misinterpreted. For example STOUT says (p. 419) "EAST and HAYES believe that heterozygosity gives an increase of both vigor and fertility in proportion to the number of heterozygous factors in the organism." There are two errors in this statement. Neither SHULL nor EAST has maintained that crossing increases fertility. The number of flowers and fruit is often increased, but no data have appeared which indicate a decreased percentage of non-functional gametes. Second, EAST and HAYES used the words "roughly proportional to the number of heterozygous factors." Leaving out the word "roughly" and taking the statement from its context, conveys a very wrong impression for it was *not* assumed that *every* germinal factor affected vigor and it was expressly stated that one could *not* assume equal effects for different factors. Again STOUT achieves a remarkable misinterpretation of the results reported in table 5 of this same paper. Here 42 inter-specific crosses are reported, of which 14 show decreased vigor (this figure should be 13 instead of 14 owing to a typographical error in reporting the first cross, *N. alata* \times *Forgetiana*, which was 125 percent of the parental average in height, instead of 25 percent). STOUT leads his readers to infer that this table is the sole basis of the conclusions regarding heterozygosis, and that the conclusions are incorrect because, as he states: "There was increased vigor in only 17 cases, but there is no apparent reason why, if it is simply heterozygosity that increases vigor, more of the combinations should not show increased vigor."

Now what are the facts. The statements on the previous page (p. 27) of the paper make it clear that many varietal crosses were made (over 100 in *Nicotiana* alone to that date), *which showed vigor equal to, or greater than the parental average*. While not expressly stated, it may

be inferred that none was found with decreased vigor. If it had been otherwise it would have been stated. Multiplication of such data was thought unnecessary in view of the exceedingly numerous results of KÖLREUTER, KNIGHT, GÄRTNER, NAUDIN, FOCKE, DARWIN and others, on the increased vigor of such hybrids. This table then, *as is shown on pages 29 and 30*, was submitted for the particular purpose of trying to establish a wholly different thesis, viz., that as germ plasms become more and more unlike, there comes a time when hybrids show (1) an inability to form germ cells (sterility), and (2) difficulty in somatic cell division. Our typographical error was unfortunate, but in view of the text given the statement made by STOUT is an inexcusable perversion of our work.

We have mentioned but two out of a goodly number of misconstructions of work with which we have been concerned. We have done this because we believe that they are paralleled in the author's criticism of most of the writers mentioned above, and because we realize that if we undertook to point out these misunderstandings in the case of other writers, the answer would be that it was merely a difference of opinion.

On the other hand, STOUT has given us a classification of types of sterility, and has reported a really immense amount of data. We hope that he will give a more constructive analysis of them later.

THE MATERIAL USED AND THE GENERAL PLAN OF THE PRESENT INVESTIGATIONS

The investigations described in this paper may be said to have been begun in 1910, when, in connection with some genetic studies on size in the genus *Nicotiana*, the two species *Nicotiana Forgetiana* (Hort.) Sand. and *Nicotiana alata* Lk. and Otto var. *grandiflora*⁹ Comes were found to be self-sterile. These two species have been made the basis of our experiments, though later some work was done upon *Nicotiana angustifolia* R. and P. var. *crispa*⁹ Cav., *N. commutata* Fisch. & Meyer, and *N. glutinosa* L., in which self-sterility had been discovered.

The characters of these species and of *Nicotiana Langsdorffii* L., a self-fertile species used, are described in COMES (1899), SETCHELL (1912), and EAST (1913, 1916).

From the technical standpoint the material has been ideal. Any combination of the three species *N. Forgetiana*, *N. alata*, and *N. Langsdorffii* can be made, the F₁ hybrids being completely fertile (in proper cross-fertile combinations). *N. glutinosa* and *N. angustifolia*, however, can

⁹ Hereafter *N. alata grandiflora* will be known as *N. alata* and *N. angustifolia crispa* as *N. angustifolia*.

neither be crossed together nor with the other species. The plants of each race grow rapidly and vigorously, and are not easily affected adversely by sudden changes in environmental conditions. They are not subject to serious parasites. Cuttings root well, and with care old roots will live through a second and occasionally even a third season. Emasculation and pollination are easy to perform, and seed production in fertile crosses is high.

N. Forgetiana, *N. alata* and *N. angustifolia* belong to the subgenus *Petunioides*, a fact worthy of note because nearly all of the species of this section have both showy flowers and abundant nectar which attract insects and thus promote cross-pollination. Even *N. glutinosa* has rather conspicuous blossoms, though belonging to the subgenus *Rustica* in which most of the species have small and unattractive flowers that are self-pollinated naturally. In other words all four of these species probably had evolved structural modifications which aided cross-fertilization long before the development of their self-sterility. We are dealing, therefore, with plants desirable both from the viewpoint of the experimentalist and of the student of evolution, a most unusual combination.

The general problem presented by this material obviously was to discover the facts regarding self-sterility, and to determine whether these facts might be fitted by a simple mathematical or chemico-mathematical description. It has been attacked along three distinct lines: (1) pedigree cultures; (2) histological studies of pollen tubes in crossed and in selfed pistils, and in inter-specific and inter-generic crosses; and (3) physiological studies of pollen tubes cultivated on artificial media.

Work along this general plan has been carried on at the Bussey Institution of HARVARD UNIVERSITY continuously since 1910, though it has not been our sole interest. It was our good fortune to have the very efficient aid of Dr. O. E. WHITE, then a graduate student and assistant at HARVARD UNIVERSITY, during the winter of 1911-12. The junior author's connection with the work began in February 1914, and has continued until the present time. In addition, Miss GRACE SHEERIN and Miss BERTHA KAPLAN have assisted in the pollination work for limited periods of time.

It being impracticable to present and to examine these various data within the limits of a single article, we propose to take up only a portion of the pedigree culture work in this paper, leaving the remaining questions to be treated later. The pedigree culture investigations have thus far involved four studies: (a) the effect of environment on self-sterility;

(b) the relations existing between self-sterile plants in intra-specific and inter-specific crosses; (c) the relations between self-sterile and self-fertile plants; (d) selective fertilization. The first two studies will be discussed here.

The usual precautions used by plant geneticists have been carefully observed, including castration of all flowers on self-sterile plants used as pistillate parents. This safeguard would not be worthy of especial mention except for the fact that it is wholly disregarded in STOUT's recent paper (1916). We shall show in a later paper that effective pollen mixed with "own" pollen causes scarcely any acceleration of "own" pollen tubes in *Nicotiana*. But we cannot find that STOUT determined this for chicory, and to take for granted that there is no such effect seems to us a laxity in a scientific work.

Every important fact described has been confirmed independently by each of us, and certain of the data that have been remarkably orderly (for example, table 11) have been collected by several persons in such a manner that personal equations were largely eliminated.

It may be noted here that a preliminary report of some of the work which we now report in detail was published in 1915 (see EAST 1915). With more data in hand more definite ideas on the subject have been possible, hence several differences will be noted between the statements made then and now. It is scarcely necessary, however, to point out every difference in the interpretations, as we shall endeavor to give in full our reasons for the present conclusions.

THE EFFECT OF THE ENVIRONMENT ON SELF-STERILITY

In beginning the description of our experiments with a section on the effect of environmental changes on self-sterility a chronological inversion is made which needs explanation, particularly as carefully planned experiments designed to show the effect of individual environmental factors when all others are controlled have not been carried out. Work on the relation between self-sterile plants was started with the idea, that even though DARWIN were correct in supposing that self-sterility is seriously affected by changes in the environment, conditions might be kept so constant that no difficulties would be encountered. Indeed, this is probably the case, since no particular difficulties were experienced during several years in spite of *certain* environmental factors being constantly varied. There came a time, however, when troubles arose which were puzzling for a considerable period. Our inquiries regarding the effect of the

environment on self-sterility have finally removed the stumbling-block and have made a clear and reasonable analysis of the pedigree culture work possible.

In brief these conclusions are as follows :

1. Self-sterility is a condition determined by the inheritance received, but can develop to its full perfection only under a favorable environment. This is not a strange conclusion, for perhaps particular environmental combinations are necessary for the full development of all positive somatic characters. But certain characters are much more seriously affected than others by the environmental variations likely to be met under ordinary conditions. For example, BAUR (1911) showed that *Primula sinensis rubra* produces red flowers when grown at a temperature of 20° C. and white flowers at a temperature of 30° C.; EAST and HAYES (1911) found that the red pericarp characteristic of a certain maize variety developed in sunlight but not in shade; Miss HOGE (MORGAN et al., 1915) discovered that in a *Drosophila* mutant with supernumerary legs the character was only called out when the animals were kept at 10° C. Self-sterility is such a character. It develops fully only under conditions which promote a normal healthy vegetative growth, and during the active part of a flowering period.

2. At the end of a flowering period and under conditions adverse to vegetative growth, self-sterility declines until a few seeds may sometimes be obtained after self-pollination. Occasionally even a full capsule is produced. The immediate cause of this partial return to a pseudo-fertility is the acceleration of pollen-tube growth that obtains under these conditions. Since we have reason to believe that the difference between a fertile and a sterile combination in these plants is the ability of the pollen grain through something inherent in its constitution to call forth in the tissue of the style in the former and not in the latter case a secretion which accelerates pollen-tube growth, it follows that in weakened style tissue some change has occurred that renders this secretion more easily produced.

3 Self-sterility can be restored in weakened plants by allowing them to go through a period of rest and then, by proper treatment, bringing them into flower anew as vigorous plants. Truly self-fertile plants cannot be forced into self-sterility by any treatment. This last conclusion is of course largely a conclusion by analogy and is not subject to rigorous proof.

4. Self-sterile races differ in their norms for self-sterility. Thus in

N. Forgetiana and in *N. angustifolia* the character is much more stable than in *N. alata* and *N. glutinosa*. In many ways this behavior indicates the existence of multiple allelomorphs for self-sterility.

The basis for these conclusions is the whole of our experience with self-sterile plants, which, it is scarcely necessary to say, cannot be cited statistically in this place. But the following facts will show, we hope, that they are well founded.

Cross No. 1 between *N. Forgetiana* and *N. alata* was made in 1909 using *N. Forgetiana* as the female. At that time both of the parents were thought to be self-fertile because a carefully bagged inflorescence of each species had yielded seed; but when the plants of the F_1 generation turned out to be self-sterile, the status of the parents was investigated more carefully. Over two hundred plants of *N. Forgetiana* have been tested under various conditions. Plants growing out of doors both on good soil and on poor soil have been tested throughout the growing season. Greenhouse-grown plants have been tested not only throughout a normal flowering period (about 3 months), but have been forced through an abnormally long flowering period during the test. Plants well nourished have been compared with plants poorly nourished, and plants well watered with plants under conditions of drouth. Both old roots and cuttings brought into a second flowering period in fine condition have been compared with much pruned old roots and cuttings in poor condition.

Only 3 cases of seed production have been observed. 2 plants at the end of their flowering period under conditions adverse to vegetative growth produced 1 and 2 capsules respectively having about 50 seed each (the normal is *ca.* 300) out of 14 tests. The third plant was not tested until near the end of its flowering period. At that time it was noted that it seemed to be self-fertile. Under test it did indeed produce several fine seed capsules after self-pollination and would undoubtedly be called a self-fertile plant were there not the following reasons for considering it an unstable self-sterile (see description of *N. alata*).

1. The plant when first tested was in a late flowering stage, yet produced capsules only in about half the tests.

2. After pruning and resting for a time the plant was brought into vigorous flower a second time. The tests during the first two weeks of this period (about 20 flowers) were all negative. The plant seemed to be perfectly self-sterile. Gradually, however, self-fertility returned as the flowering period waned.

3. Twenty-four plants grown from selfed seed of this individual, tested during the height of their flowering period, all proved self-sterile.

We are therefore forced to concede the probability that an error of manipulation or of record was made in 1909, although we may have happened upon a plant like the one just described since the original selfing was done at the end of the flowering season. Be that as it may, the conclusion is inevitable that *N. Forgetiana* (and *N. angustifolia* has

TABLE I

Progeny of pseudo self-fertile N. alata plant used in cross No. 2. Grand-progeny of original pseudo self-fertile plant. Subscripts show number of pollinations made.

Ped. No. ♀	No. selfings sterile	No. selfings giving capsules			Plants with which cross- fertile ♂	Plants with which cross- sterile ♂
		1-10 seeds	10-50 seeds	250-300 seeds		
53	6		1		57	54 ₂
54	5					53 ₂ , 57 ₂ , 58 ₂
56				3		53, 57, 58, 59
57	3					58
58	1				53, 59	314
59	2					314, 53, 54, 56 ₂ , 57 ₂
61	3					
62	4	4		2		58, 79
64	3	1				58
65	6					79
66	12	1				58, 62, 71, 79
67	3					
68	4					
70	5	1	1			
71	3		1	1		314, 58
72	3					
73	4					
74	1					
75	8					
76	2	1		2		66
77	2					
78	9					66
79	3	1				58, 66

1 pollination 53 × 54 and 2 pollinations 59 × 53 produced 1-10 seeds each.
314 = *N. Forgetiana*.

yielded similar results) is a self-sterile species of remarkable stability, which only occasionally (1 in 300?) produces a plant that shows some self-fertility under adverse conditions.

N. alata, on the other hand, has proved to be more unstable¹⁰ in its self-sterility; or better, it has proved to have a norm more nearly inter-

¹⁰ *N. glutinosa* appears to behave like *N. alata*, but has not been tested very thoroughly.

mediate between the extremes complete self-sterility and perfect self-fertility. But fundamentally it is a self-sterile species like *N. Forgetiana*.

Numerous *N. alata* plants have been tested for self-sterility under the same conditions as described above for *N. Forgetiana*. The results have been similar in that the plants were practically always completely self-sterile during the early part of a vigorous flowering season. But under adverse conditions during the latter part of the flowering period, rather a high percentage of the plants produced capsules with from 1 to 50 seeds each. Only 2 plants have been found, however, that appeared to be almost completely fertile from the middle of the flowering period onward under normal conditions. Of these plants more is to be said.

Assuming that no mistake was made in 1909 and that selfed seed was actually obtained from a field-grown plant of *N. alata*, we have records of its progeny for three generations.

Twenty-five seedlings from this seed were grown in 1914. These plants were tested for self-sterility as field-grown plants, though not as thoroughly as might be desired. 2 plants showed some self-fertility,—no tests having been made until the latter part of August. From 1 of them selfed seed was obtained and a second generation grown. 23 of these plants were tested in the greenhouse with the results shown in table 1.

Fourteen of these plants produced no seed when selfed; 9 showed some degree of self-fertility. This fertility apparently occurred only

TABLE 2
Progeny of pseudo self-fertile N. alata plant No. 56.
Great-grand-progeny of original pseudo
self-fertile plant.

Ped. No.	No. selfings sterile	No. selfings giving capsules		
		1-10 seeds	10-50 seeds	250-300 seeds
80	9	2	2	
81	1			
83	7			
84	3			
85	10	2	1	1
86	1			
87	5			
89	7			
90	8			
91	8		1	
92	1	1		
93	8		2	
94	4			
95	3			

when the flowering season was waning and the plants were under adverse conditions, as was stated before; but it cannot be proved that this was always the case, for one cannot draw a definite line between vigorous and weakened plants. 3 plants, excluding No. 56, produced some full capsules, but in these cases the remaining self-pollinations and sterile cross-pollinations show that the plants were not truly self-fertile. Plant No. 56, however, showed no direct indications of self-sterility in connection with the 3 self-pollinations tried. More pollinations should have been made on this plant at the beginning of a second flowering period. Unfortunately, it was discarded. The evidence of self-sterility, therefore, is wholly circumstantial. It is, that though having functional ovules No. 56 was sterile to the pollen of plants 53, 57, 58 and 59, and though having functional pollen it was sterile crossed on plant 59.

A small population was grown from the selfed seed of this plant. It is shown in table 2.

Although 5 of the plants produced some seed, if one considers the date of manipulation and the state of the plants, the evidence is all in favor of the idea that this was an effect of external conditions. There is no reason whatever for believing that any of the plants were truly self-fertile.

All told then, we have three generations of *N. alata* plants, each generation being grown from selfed seed produced from plants apparently weakened at the time of seed production, without the occurrence of a single plant which behaved in every way like a truly self-fertile individual. It seems to us, therefore, that this selfed seed might be thought of as having been produced artificially.

If this be the correct view of the matter, it is clear that there is no reason why fusion between gametes produced by a self-sterile plant cannot occur provided the male generative nucleus enters the embryo sac. Such unions may take place without affecting the self-sterility of the progeny. Even by the selection of apparently self-fertile plants for three generations no tendency toward the formation of a self-fertile race is indicated. Just how broadly one may generalize from these data is still problematical, but the two following conclusions are certainly more than guesses.

(1) Unless a male gamete complementary to every female gamete is formed, there is no selective fertilization, for *full* capsules have been found on plants that in the early part of the season and in crosses showed they were really self-sterile. Other evidence militating against selective

TABLE 3
Progeny of N. alata No. 58 × N. alata No. 56.

Ped. No.	No. selfings sterile	No. selfings giving capsules		
		1-10 seeds	10-50 seeds	250-300 seeds
96	5	1	3	
97	5	1		
98	11	1		
99	4			
101	4			
102	4			
103	8			
105	8		2	
106	7			
107	3			
108	4			
109	1	3	2	
110	3			
111		3		
113	1			
116	4			
117	6			
118	7			
119	3			
120	5	1		
121	2			
122	7			
123	5	1		
124	5			
126	1			
127	8			
128	4			
133	1	3		
135	3			
136	3	2		
137	3			
139	9	3	1	
140	4			
141	2			
144	4			
146	6			

fertilization which will be presented in a later paper has also been obtained by a different method of attack.

(2) It follows therefore that self-sterility behaves as a sporophytic character and is not the result of incompatibility between gametes.

One other bit of evidence regarding *N. alata* should be presented here. It is the behavior of the progeny of a cross between the self-sterile plant No. 58 and the apparently self-fertile plant No. 56. These data are reported in table 3.

Here again we find a considerable percentage of plants, a third to be exact, giving a few capsules having from 1 to 50 seeds each. Here again

it was the plants near the end of their flowering season, the plants that had been cut back strongly, the plants that were producing flowers on one or two weakened branches, that gave the seeds. To be sure, as in other families, one or two plants apparently vigorous behaved in the same way near the end of the flowering season. But the correlation between *weakened failing* branches at the end of their flowering period and *tendency toward self-fertility* was very high even when judged only by external appearances.

The remaining data on this subject cannot be discussed in this place without repetition, since they include nearly all our pedigree culture work. And at any rate they are important only as corroborative evidence, for in our regular experiments extremely weak and old flowering branches were seldom used. For this reason we rarely had to contend with any approach toward self-fertility in self-sterile plants. But the phenomenon when met lent support to our hypothesis. Furthermore, *cross-sterile combinations behaved in the same way*.

These conclusions have been a great aid to us in analyzing our pedigree culture facts. Without them the data from two or three of our populations, where pollinations were carried on up to the end of the flowering season, would have been somewhat chaotic. They reveal, for example, that *N. alata* is just as much of a self-sterile species as *N. Forgetiana* though the expression of the character is affected more easily by external conditions. They show clearly why selection for three years accomplished nothing. The selected extreme was a non-inherited fluctuation. It is clear also why crosses between these apparently self-fertile plants and plants unquestionably self-sterile, yielded no truly self-fertile offspring in either the F_1 or F_2 generations. The plants were really self-sterile; they were pseudo-fertile, and will be so called.

In this connection it may be recalled that DARWIN (1876) found that self-sterile plants of *Abutilon Darwinii* became partly self-fertile *at the end of their flowering season*.

Keeping these things in mind, one is able to classify the pedigree culture results with great accuracy, though there are five possibilities of error.

1. There may be error of record. This we believe to be slight, owing to our various methods of checking results.

2. A true sterility either partial or complete may exist. This usually can be discovered by a microscopical examination of the pollen, and may be tested by reciprocal crosses. The reciprocal cross test has never

brought to light a case of ovule sterility and pollen fertility, but the converse is sometimes true.

3. Combinations made but once and failing must be reported as sterile; but this is an error about 4 times per hundred, since this is the ratio of failure found in combinations known to be fertile, by reason of an imperfect technique or other unknown causes. We cannot correct accurately for this error, but it must be considered when discussing exceptions to a general scheme which other data fit.

4. Combinations may fail once and succeed once in two trials, or in very rare cases fail twice and succeed twice in four trials. Experience has shown that if the capsules are normal in size and full of seed, the combination is fertile. Fertile combinations *always* give full capsules. There is no partial fertility in fertile combinations except as *true* sterility exists in some degree (see error 2). Conversely, it is possible of course to meet with a pseudo self-fertile plant like *N. alata* plant No. 56, which under adverse conditions might give full capsules of normal size after a "sterile" combination had been made. But under the environmental conditions that usually obtained during our work, this would be extremely rare,—to the best of our knowledge and belief not over 1 per 200 plants.

5. Combinations may give capsules with from 1 to 50 seeds as well as failures. These are sterile combinations. They probably occurred in only three families, because only in these families were the plants utilized during the *whole of their flowering period*. Unfortunately it must be admitted that a few errors of record may have been made with these cases. A small number of apparently successful matings were not recorded until the capsules had opened. Since the capsules were of normal size and each had contained a number of seeds, these combinations were recorded fertile, but the matter is not certain.

It is not believed that these errors are serious even when taken together but some allowance must be made for them in considering the few exceptions noted in the analyses we have made of the tables that follow.

INTER-SPECIFIC PEDIGREE CULTURE EXPERIMENTS

All of the crosses reported in this paper are between species or varieties believed to be self-sterile for the reasons set forth in the foregoing section. But because certain plants were used which under the peculiar conditions at the time of the test for self-sterility yielded some selfed

seed, these plants are distinguished by the term "pseudo self-fertile." Their behavior in these crosses is further evidence that the term is justified.

Cross No. 1. N. Forgetiana \times *N. alata* (self-sterile \times self-sterile)

The cross to be described first is that mentioned previously in connection with the discovery of self-sterility in the genus *Nicotiana*. It was made in 1909, using *N. Forgetiana* as the female and *N. alata* as the male.

The F_1 generation

The F_1 population consisted of vigorous plants twenty-five¹¹ percent taller than the average of the two parents and was extremely uniform in size and in color of flowers, though the latter were not so dark a red as those of the male parent. A few individuals tested for fertility in 1910 and others from the same original cross again tested in 1912, all proved to be self-sterile. The actual tests made, some 20 plants altogether, were too few to claim self-sterility for every individual, but careful observation of about 50 other plants in the field indicated this to be the case. These observations were made by estimating the number of capsules which developed naturally on each plant, it having been determined that on self-fertile plants of an allied species, *N. Langsdorffii*, from 10 to 20 times as many capsules develop as on self-sterile plants of *N. alata*, though the ratio of flowers formed on the two species is only about 3 to 1.

No extended experiments were carried out to test the fertility of these plants in intercrosses. 6 intercrosses between sister plants were made and each was successful, but whether some cross-sterility existed or not is unknown. The pollen, however, was good in every plant examined (about 30).

The F_2 generation

From these 6 intercrosses between pairs of F_1 plants almost a thousand individuals were grown. They showed a most remarkable variation in all their characters, the range including the modal values of both grandparents. The frequency distributions for length and for breadth of corolla have been discussed in another paper (EAST 1913), and it will suffice to note here that while the coefficient of variation for length of corolla in the F_1 generation was $8.28 \pm .38$ percent, in the F_2 generation it was $22.57 \pm .39$ percent.

¹¹ By a typographical error the height of this cross is made 25 percent instead of 125 percent in table V, EAST and HAYES 1912.

There was also a great range in color of corolla, which even with the considerable number of subsequent generations grown, has not been analyzed to our complete satisfaction. 4 Mendelian factors appear to describe the breeding results best, giving the 7 forms, red, magenta, light red, light magenta, light red on exterior of corolla only, light magenta on exterior of corolla only, and white. Red is epistatic to magenta, and the darker colors are epistatic to the lighter ones.

These details are given in order to emphasize the fact that here we have two races sufficiently distinct from each other to be designated as separate species, which cross easily and give a fertile F_1 generation and a wide range of forms in the F_2 generation. The fertility of the F_1

TABLE 4
Result of matings on 20 plants of the F_2 generation of cross No. 1
N. Forgetiana \times *N. alata*.

		Plants used as males																			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Plants used as females	1	S	F					F			F	F									
	2		S								F	F	F							F	
	3	F	S			F		F			F	F			F		F				
	4			S				F			F	F									
	5	F			S		F	F	F	F	F	F	F	F	F	F	F	F	F	F	F
	6				F		S		F			F		F	F			F			
	7			F				S				F				F		F			
	8	F	F	F		F	F	S		F	F	F	F	F	F	F	F	F			
	9				F				F	S			F		F						
	10					F		F		S	F	F	S	F	F	F	F				
	11						F		F		F	S	S	F	F			F			
	12			F		F					F	S	S	F	F	F	F	F	F	F	F
	13							F				F	F	S		F		F			
	14			F				F	F				F		S			F			
	15				F			F			F	F				S					
	16				F					F	F	F		F		S		F	F		
	17				F					F	F	F	F		F		S				
	18				F		F	F			F	F						S	F		
	19			F		F			F						F			F	F	S	
	20					F			F				F								S

generation indicates absence of any selective elimination of gametes or zygotes in its daughters, and the variation exhibited by these daughters shows conclusively that the original parents really did differ by a considerable number of hereditary factors. These matters are important in connection with the inbreeding experiment that followed.

About 40 plants from the F_2 generation were crossed and selfed on a rather large scale. One of these experiments in which 20 plants coming from 2 intercrosses between F_1 plants were used, is shown in table 4. The vertical columns give the number of the plants when used as males; the horizontal rows are the same plants when used as females. The result of each mating made is denoted by the letters F for fertile and S for sterile.

It was planned to make all possible combinations of these plants; but this proved to be impracticable, and only 154¹² were accomplished. The pollinations on the plants of this generation as well as those on the succeeding generations included in this experiment were made under various conditions of sunshine, temperature, moisture, food supply and age, but these variables appeared to have no influence on fertility. The results always checked. A small number of matings were made in the open field in August and September, 1911. The remainder were performed in the greenhouse. A part of these were made upon some of the old plants that had been transplanted during the late fall, and the others upon cuttings from the plants in the field which were again ready for operation in April, 1912. *But in all the work on the 20 plants tabled it should be noted that pollinations were made during the height of the flowering period when the plants were in good condition. Nevertheless, there may have been errors. If such did occur, cross-fertility would have been favored; since at the time the work was done upon the F_2 , F_3 , and F_4 generations of this cross, pseudo self-fertility was not suspected.*

The plants were each selfed from 2 to 10 times, an average of 4 times per plant, without a single seed being obtained.

Of intercrosses, 132 were made. 3 of these are indicated by question marks on the table. This is because plant 5 had defective pollen, it being the only one of the twenty in which the pollen did not show from 90 to 100 percent of morphologically perfect grains. None of the crosses where this plant was used as the male gave capsules over half-filled with

¹² A few of the figures given here differ from those given in the preliminary report on this work (EAST 1915). This is due to rechecking the results and to the addition of a few more data. There have been no essential changes and the present figures are believed to be correct.

seeds, but since 7 matings had from 30 to 100 seeds per capsule, and since the reciprocal matings were all successful we have classed them as fertile. The matings questioned, 11×5 , 14×5 , and 20×5 , ought also to be classed as fertile, since the reciprocals were fertile, but as they yielded only 2 to 10 seeds per capsule, they have been omitted from these next calculations.

Of the remaining 129 intercrosses, 126 were successful; 4 of them produced capsules having less than 50 percent of the ovules fertilized (2 pollinations each being made), the remainder produced full capsules. There were few failures among these intercrosses, though from 2 to 12 repetitions of the matings were made in almost every case. It seemed as though an intercross possible at one time could be made at any other time at the first attempt. In other words, there seemed to be no variability in ease of cross-fertilization. The failures in the fertile intercrosses were less than 4 percent, and these were complete failures which may be attributed to the technique used.

Twenty-eight intercrosses between these plants and other plants of the F_2 generation were also made with 28 successes. In addition, 92 other combinations were made between plants not shown in the table. They are not reported in detail because only a few matings per plant were made; but the gross results were 89 successes and 3 failures.

Altogether among these matings there were 54 pairs of reciprocals each of which gave the same result.

The failures in the intercrosses remain to be considered. The table shows 3 cases; of which 10×13 was tried 2 times; 11×12 , 12 times; and 12×11 , 6 times. The last pair are reciprocals, but we shall treat reciprocals separately for the present. Of the other 3 cases, 2 of them were tried 3 times, but the third was made only once, which of course does not settle the matter. Thus there were 4 definite cases, 1 probable case, and 1 questionable case of cross-sterility, a matter of 2.4 percent (6 out of 249).

The F_3 generation

Out of the many fruitful combinations of F_2 plants, 29 F_3 families were grown,—50 to 150 individuals of each being transplanted from the greenhouse to the field with due care that random samples were obtained. Field examinations as described above, indicated a total absence of self-fertile plants, and from 3 to 6 attempts to self individuals of each family resulted in failures.

The progeny of 2 red-flowered plants of the F_2 generation furnished

TABLE 5

Result of matings on 12 plants of the F_1 generation of cross No. 1,
N. Forgetiana \times *N. alata*.

		Plants used as males											
		1	2	3	4	5	6	7	8	9	10	11	12
Plants used as females	1	S		F	F	F		F		F		F	
	2		S		F	F		F		F	F	F	F
	3	F		S		F		F			F	F	
	4	F	F		S		S		F	F	F		
	5			F		S			F	F		F	F
	6	F		F	S	F	S		F	F	S		F
	7	F	F	F		F	F	S	F	F		F	S
	8			F	F	F		F	S		F	F	F
	9	F		F		F	F			S		F	F
	10			F	F	S	S	F	F		S	F	
	11	F		F	F			F	F		F	S	F
	12							F			F		S

the material for the continuation of our intercrossing experiment. Most of the work was done on 12 plants as set forth in table 5. Fruitless self-pollinations averaging over 3 per plant proved they were self-sterile. 102 cross-pollinations were made: 75 are shown in the table; 27 were made in a less systematic manner with 11 other plants of the same family. These resulted in 95 successes and 7 failures. Again the "possible" combinations were almost always successful. The unsuccessful matings were 4×6 , 6×4 , 6×10 , 10×6 , 7×12 , and 10×5 . Combination 6×4 was made twice and combination 7×12 once, the remainder were made three or more times. The first 4 matings consist of 2 pairs of reciprocals. The reciprocal of 7×12 was also made, but proved to be fertile. This is evidence that with further trials 7×12 would also have been successful, for we have *invariably* found reciprocals to behave alike when a number of pollinations sufficient to determine definitely the status of the cross has been made. In fact 26 reciprocals gave the same result in this population. The remaining combination showing cross-sterility was between plants 21 and 27. Eliminating combination 7×12 , therefore, 6 percent gross of cross-sterility is shown in the F_3 generation.

The F_4 generation

Only 2 of the F_3 combinations were grown during the next season and the pressure of investigations along other lines was such that but little work was done upon them. Field examination and tests on 21 plants, however, showed us no self-fertility. 10 of the progeny of 2 red-flowered F_3 plants, had 52 matings made upon them, 15 being reciprocals giving duplicate results. In addition 6 random matings with other plants of the family were tried with 1 failure. There were 48 successful and 4 unsuccessful matings on the 10 plants shown in table 6. The fertile matings yielded good capsules as usual with 3 exceptions, there being but 7 complete failures out of over 200 pollinations. Of the unsuccessful combinations, pollinations were made as follows: 2×8 , 4 trials; 5×2 , 6 trials; 5×8 , 4 trials; 8×5 , 5 trials; and 8×12 , (not shown in the table) 4 trials. Each of these cases is fairly certain, therefore, and gives us a gross cross-sterility ratio of nearly 9 percent.

The F_5 generation

Only 1 F_5 family was studied, but as it was planned to discontinue this particular experiment, considerable attention was given to it. As was also true of the F_3 and F_4 generations, the work was carried on under field conditions. Similarly again, it was produced by mating two red-flowered sibs.

A random sample of 20 plants was marked for work, and 439 pollinations made (table 7). Of these pollinations 92 were wholly unsuccessful attempts to secure selfed seed made on 17 plants, an average of 5.5 pollinations per plant. Thus there is no question about the self-sterility of each plant tested. Plants 4, 5 and 20 were not tested. Plant 4 had such bad pollen that results with it are valueless, and plants 5 and 20 were somewhat sickly. Plant 9 also had such poor pollen that the seed capsules were not full, but a classification of the matings where it was used could be made without any serious chance of error. 274 pollinations were made on the 119 intercrosses that proved fertile. Only 12 of these attempts failed, and 5 of them were on crosses between No. 9 and No. 3. Thus only 4 attempts per hundred failed in the intercrosses that were classed as fertile from records of other pollinations, showing conclusively, we think, that inbreeding had produced no quantitative diminution in fertility among "possible" combinations, the percentage of failures in fertile crosses in the F_2 generation being about the same.

The remaining 73 pollinations were unsuccessful attempts to obtain seed in 33 intercrosses. The details are shown in table 8.

TABLE 8

Record of unsuccessful cross-pollinations made on the F_5 generation of cross No. 1, Nicotiana Forgetiana \times N. alata.

Mating	Pollinations	Mating	Pollinations	Mating	Pollinations
1 \times 4	1	7 \times 9	1	16 \times 20	3
2 \times 4	1	7 \times 10	1	17 \times 8	2
2 \times 5	1	7 \times 11	1	17 \times 11	2
2 \times 16	2	9 \times 5	3	17 \times 12	3
2 \times 17	2	10 \times 5	1	18 \times 3	3
2 \times 20	3	12 \times 8	3	18 \times 7	3
3 \times 10	2	13 \times 3	2	18 \times 10	3
10 \times 3	2	14 \times 6	3	18 \times 11	3
3 \times 11	2	15 \times 6	3	18 \times 13	2
7 \times 3	3	15 \times 14	2	19 \times 5	2
7 \times 4	3	16 \times 9	1	19 \times 20	4

It will be seen that only 1 reciprocal cross was made on these plants and this was by accident. A large number of reciprocals had been made on other crosses always with the same results when tried a sufficient number of times to make classification conclusive. It was decided therefore, to make as many distinct matings as possible in order to make a thorough test of the mating proclivities of the plants under observation. The result is that the percentage of cross-sterility found in the F_5 generation is not strictly comparable with the percentages found for the earlier generations where matings were made at random and each mating counted. To be sure a few reciprocal matings¹⁸ were made in F_5 , but the percentage is very much less than in the preceding generations. The gross cross-sterility found in F_5 was 21.7 percent, if the 8 crosses where only 1 pollination was made be counted. By the theory of error 1 of these cases might be excluded, while for certain other reasons (see table 9) error is suspected in another case, but since this correction would reduce the cross-sterility percentage by only 1.2, the figures 21.7 will be allowed to stand.

Eight other intercrosses between other plants of this same population were also made. We have not thought it necessary to include them in the table because the attempts at crossing were so sporadic, but the percentage of cross-sterility would scarcely be changed, for 7 out of 8 intercrosses were fertile.

A number of other facts appear in the data shown in tables 7 and 8, which are not apparent without careful study. In accordance with their behavior in intercrosses, the plants may be grouped into 5 classes in

¹⁸ Seven reciprocals were made altogether in this family with like results.

which there is intra-class sterility and inter-class fertility, with very few exceptions. This grouping is shown in table 9. The two columns at

TABLE 9
Plants of F_2 generation of cross No. 1, $N. Forgetiana \times N. alata$, grouped in accordance with their behavior in intercrosses.

Group	Ped. No.	Number cases fertile within group					Number cases sterile within group				
		A	B	C	D	E	A	B	C	D	E
A	3	0	5	2	3	1	5	0	0	0	0
	7	0	4	3	3	1	4	17	0	0	0
	10	0	3	3	3	1	3	17	0	0	0
	11	0	4	3	1	1	3	1	0	0	0
	13	0	5	3	2	1	2	0	0	0	0
	18	0	5	3	3	-	5	0	0	0	-
B	2	5	2	2	1	1	0	3	0	1	0
	5	4	1	2	3	1	17	3	0	0	0
	9	5	1	3	2	1	17	2	0	0	0
	16	6	2	3	3	1	0	3	0	0	0
	19	6	2	3	3	-	0	2	0	0	-
	20	-	0	1	-	-	-	3	0	-	-
C	6	5	4	0	3	1	0	0	2	0	0
	14	6	5	0	3	1	0	0	2	0	0
	15	6	5	0	3	1	0	0	2	0	0
D	8	4	4	3	0	1	0	0	0	2	0
	12	6	5	3	0	1	0	0	0	2	0
	17	4	3	3	0	1	1	1	0	2	0
E	1	5	4	3	3	0	0	0	0	0	0

the left show the division into groups, and the pedigree numbers of the plants within each group. The next 5 columns show the number of individual cases of cross-fertility within each group. For example, plant No. 3 was fertile with 5 plants of group B, with 2 plants of group C, with 3 plants of group D, and with the single plant comprising group E. The last 5 columns show the number of individual cases of cross-

sterility within each group. The exceptional cases where there is inter-class sterility or intra-class fertility are printed in bold-face type. By utilizing the mating record of a plant either when used as a male or female in making the classification, all of the plants could be grouped excepting number 4 which had very bad pollen. It is excluded on this account.

The number of exceptions appear at first sight to be rather large but it must be remembered that one exceptional mating makes two irregularities appear in the table. If 7 is sterile with 9, 9 is sterile with 7, for example, and both exceptions are noted.

Number 2 and number 17 are anomalous plants; the remainder behave very regularly. 2 is sterile with 17 where one would expect to find fertility: this is also true of the mating 17×11 . Both of these matings were made twice, which establishes the sterility rather definitely. In addition 2 is fertile with both 9 (thrice) and 19 (twice) of the same group, though it properly belongs in group B from its sterility with 5, 16 and 20, and its fertility with at least 1 plant of each of the other groups. The mating between 2 and 9 was fertile only 3 times in 6 trials, however, and may indicate a *pseudo-fertility due to external conditions*. The cross was made reciprocally; 2×9 was fertile in both trials, but 9×2 was fertile but once out of 4 trials.

Eliminating plants 2 and 17 from consideration, there are left only 4 unconformable matings. There are 2 cases of inter-class sterility, 9 with 7 and 10 with 5. Each of these matings was made but once, however, and their sterility is questionable because 4 times per 100 one obtains no seed in matings that otherwise prove fertile. The exceptional fertile matings, 5 with 16 (thrice) and 16 with 19 (twice), on the other hand, appear to be definitely established.

If one admits the possible fertility of combinations 9×7 and 10×5 , then, 16 plants allow themselves to be grouped into five classes A, B, C, D, and E, with no anomalous behavior whatever. Each is cross-sterile with every plant of its own class and cross-fertile with every plant of every other class with which it is tested. True, 3 anomalies remain, plants 2, 16 and 17. Number 17 of class D shows a perfectly regular behavior except with plant 11 of class A and plant 2 of class B. Plants 2 and 16 show their irregularities only within their own class except in the cross between 2 and 17, which leads us to suspect pseudo-fertility.

The conclusion seems just, therefore, that this grouping is real and significant, since the great majority of these plants (in this sample of the population, 84 percent) shows an absolutely regular behavior and the small minority of exceptional plants presents but a few irregularities.

If one admits the justice of this classification there comes the question of the number and composition of such groups in the F_2 generation of this cross. 19 plants form a very small sample of such a population. What is the composition of the whole population? The first thing to be noted is the varied size of the groups. The number of individuals in each class is 6, 6, 3, 3, and 1, respectively. Even with a due allowance for the smallness of the sample, it is clear that there is little probability of the plants being distributed in equal-sized classes. It is hardly more probable that the distribution will fit a Mendelian $(\frac{3}{4} + \frac{1}{4})^n$ expansion. It is reminiscent, however, of a normal binomial expansion $(\frac{1}{2} + \frac{1}{2})^n$. The resemblance is possibly illusory, but 0, 3, 6, 6, 3, 1 is too much like 1, 5, 10, 10, 5, 1 to escape notice, particularly as on the theory of random sampling it is possible for the whole population to contain from 1 to 3 more classes. Be that as it may, we can certainly conclude that the F_2 generation of this particular cross contains *no more* than from 6 to 8 groups—the chances are practically negligible that there might be 10—which are intra-class sterile and inter-class fertile, and within which the distribution of individuals bears some similarity to that of a normal frequency distribution.

Let us now consider whether a possible meaning can be attached to the results obtained in this experiment.

Argument on cross No. 1

We early assumed a working hypothesis in part similar to and in part different from that of MORGAN, viz.; first, self-sterility is heritable; second, as regards that part of the constitution of pollen grains which affects the behavior of self-sterile plants all pollen grains produced by each plant are alike, i.e., with reference to self-sterility pollen grains behave as if they were sporophytic; third, under normal conditions the pollen tubes produced by pollen from any self-sterile plant will not grow in styles of that plant with a rapidity sufficient to reach the ovules during the "life" of the flower, on account of this "likeness" of constitution; fourth, pollen tubes will grow with a rapidity sufficient to allow fertilization to occur if the constitutions of the two proposed parental plants *differ* from each other in any of these essential factors, by reason of a stimulus possibly analogous to that which makes growth more vigorous in first generation hybrids.

The first assumption has been demonstrated more or less clearly by all who have worked upon self-sterile plants. It is proved for self-sterile *Nicotiana* species both by the experiments reported here, and by

those to be published later on the relation between self-fertile and self-sterile plants.

The second assumption is proved circumstantially by the fact that reciprocal matings always duplicate each other. Direct experiments showing that selective fertilization does not occur have also been made, and will be the subject matter of another paper.

If there be any justification for the third and fourth assumptions, a cross between two self-sterile species differing by a large number of hereditary factors (expecting some of the differences to be effective) should show a high degree of cross-fertility in the F_1 and F_2 generations, followed by an increasing percentage of cross-sterility in later generations produced by the closest possible inbreeding. The reason for such a belief is, of course, the well-known fact that inbreeding increases homozygosis. Such being the case, plants ought to appear with "like" constitution as far as the factors affecting cross-fertility are concerned, and these should be cross-sterile to each other. If the factors affecting cross-fertility are relatively few in number, a small number of intra-sterile, inter-fertile groups should be found after a comparatively limited amount of inbreeding. This, broadly speaking, we believe to be a plausible interpretation of the facts found. A detailed interpretation is given later.

In general, the F_2 generation of such a cross—between species—might be expected to show an approach to the maximum limit of cross-fertility, since the F_2 generation usually shows greater variability than succeeding generations. But in the case of self-sterility where the self-sterile plants must be supposed to differ in constitution among themselves, this is probably not strictly true. If one could test a large series of F_2 populations from various original and F_1 matings, he ought to find a variable degree of cross-fertility, with the maximum reached only in certain cases.

In this instance, no claim can be made that we are dealing with the maximum. We can only report the results for this case, pointing out that in crosses No. 2 and No. 3, the cross-fertility is much lower.

One of the best systems of inbreeding in the case of self-sterile plants is to mate sister plants in successive generations, for such crossing, after an original mating $Aa \times Aa$, by Mendelian recombination ultimately gives a population in which AA and aa each approach $\frac{1}{2}$ and Aa approaches 0. Expectation of homozygosis in successive matings is $\frac{1}{2}$, $\frac{5}{8}$, $\frac{11}{16}$, $\frac{31}{64}$ - - - I (JENNINGS 1916). This system seemed to suit

our purpose better than any scheme of mating parent with offspring, because of the difficulty of keeping plants alive for several years.

It is regretted that so little is known about the cross-fertility of the F_1 generation, but this bit of ignorance does not affect our test seriously. This really begins with the inter-cross of two self-sterile F_1 plants, which were similar in appearance, but were producing numerous different types of gametes, as is proved by the extremely variable F_2 generation.

The cross-sterility¹⁴ of the F_2 generation was 2.4 percent, if the sixth case of sterility where only one pollination was made, be included. The result on the 20 plants tested rather thoroughly was 3 cases of cross-sterility out of 131 matings. The result on the other twenty-odd plants tested less thoroughly was 3 cases of cross-sterility out of 120 matings. And this percentage of cross-sterility may have been too low, as was mentioned before, because of our failing to suspect pseudo cross-sterility at this time. But taking this low estimate of cross-sterility at its face value, it is clear that no hypothesis of Individualstoffe (Cf. Jost 1905) is necessary to account for the results. The presence of even 6 cases of cross-sterility in 251 matings eliminates this requirement definitely.

The number of classes which would be necessary to give such an amount of cross-sterility, on the assumption of inter-class fertility and intra-class sterility, depends upon what is presupposed as to the frequencies within the classes.

As we shall have a number of such estimations to make, let us consider the matter here. It is always dangerous to calculate *a posteriori* probabilities. But because this danger is realized, and the probabilities calculated must be used with caution, it seems best to use as simple an approximation as possible. Therefore, we have assumed that if S and F represent the total number of sterile and of fertile matings found, the

probable error of the determination $\frac{S}{S+F}$ is $\pm \frac{.6745}{S+F} \sqrt{\frac{(S)(F)}{S+F}}$. In obtaining this figure, self \times self is added to the cross-sterility of course, S representing the total of sterile combinations. The fraction $\frac{S}{S+F}$ then gives us a measure of the probable number of classes for

¹⁴ In our preliminary paper (EAST 1915) judgment was withheld as to the validity of the apparent cases of cross-sterility in the F_2 generation of this cross. The recovery of a misplaced data card with records of duplicate cross-pollinations made on the combinations that had shown apparent cross-sterility, by Dr. WHITE, gives us the grounds for our present conclusions,

$\frac{S}{S+F} = \frac{\Sigma(C_a^2 + C_b^2 + \dots C_r^2)}{\Sigma(C_a + C_b + \dots C_r)^2}$, where r is the number of classes, and C_a, C_b , etc., are the number of individuals within each class.

If the classes are of equal size, the ratio of sterility to total number of combinations is $\frac{1}{n}$ where n is the number of classes; for if there are x individuals in each class the sterility is $\frac{nx^2}{n^2 x^2} = \frac{1}{n}$. If on the other hand, the distribution of individuals within the classes is that of the coefficients of the point binomial, these coefficients must be substituted.

With these two assumptions as to distribution, the following percentages of sterility to total number of matings is found:

Number of classes	Equal size	Point binomial	Number of classes	Equal size	Point binomial
4	25.0	31.3	15	6.6	15.0
5	20.0	27.3	16	6.2	14.5
6	16.7	24.6	17	5.9	14.0
7	14.3	22.6	18	5.6	13.6
8	12.5	20.9	19	5.3	13.2
9	11.1	19.6	20	5.0	12.8
10	10.0	18.5	21	4.8	12.5
11	9.0	17.6	22	4.5	12.2
12	8.3	16.8	23	4.3	11.9
13	7.7	16.1	24	4.2	11.7
14	7.1	15.5	40	2.5	9.0

Should one wish to make the calculation from cross-sterility only on account of the self-sterility determinations being selected values the formula becomes

$$\frac{S_c}{S_c + F} = \frac{\Sigma(C_a^2 + C_b^2 + \dots C_r^2) - \Sigma(C_a + C_b + \dots C_r)}{\Sigma(C_a + C_b + \dots C_r)^2 - \Sigma(C_a + C_b + \dots C_r)}$$

but this correction is unnecessary under most circumstances.

Taking now the gross returns on the F_2 generation at their face value, 2.4 percent cross-sterility, or 15.8 percent total sterility on the 40 plants used, the number of classes of approximately equal size necessary to account for the results is between 8 and 14. But the groups which were afterward found in the F_3 generation, were not of equal size. Their frequencies resembled rather those of a point binomial. Assuming such a distribution within the classes of F_2 , the number of classes would lie between 12 and 25.

These class number determinations have been made roughly on purpose. There are three reasons for doing this.

In the first place, there is reason to believe that the proper percentage of cross-sterility was not obtained. Our calculations were made by including with the matings listed in table 4, 28 matings of plants shown in table 4 with other plants, and 92 matings made rather unsystematically between about 20 plants not shown in that table. Data as to the age, condition, flowering period, etc., of these plants were not recorded. Furthermore, fertility and sterility were usually recorded merely as *F* and *S* without data as regards the percentage of seeds in the capsules. For our present purpose, therefore, they have *not* the value of the data recorded in table 4.

Probably the correct way to treat the data of table 4 would be as follows. Consider every mating as if it were made reciprocally whether actually accomplished or not. For example, 5×1 is fertile; then assume 1×5 to have been fertile even though that mating was not attempted, since reciprocals always have given the same results. If this be done the records show 184 cases of cross-fertility, 4 cases of cross-sterility and 20 cases of self-sterility. Another question then arises. These plants supposedly were *all* in good condition and in general were mated only at the height of the flowering season. But we did not at that time suspect pseudo cross-fertility, and made no particular attempt to clear up doubtful cases, as was done later on crosses No. 2 and 3. Now crosses 3×17 , 5×15 , 6×8 and 19×14 , although made twice each, showed less than 50 percent of the ovules fertilized. The reciprocal of 6×8 was clearly fertile, so this mating remains in the "fertile" column. But there is good reason from analogous results in the other families for considering the other 3 matings as sterile. The mating 5×15 may be questionable, but as 5 had such bad pollen we cannot be certain of the placing of mating 15×5 , as was stated earlier. If then we remove these matings from the fertiles to the steriles, which seems the logical thing to do, there are 178 cases of cross-fertility, 10 cases of cross-sterility and 20 cases of self-sterility. The total percentage of sterility is 14.4 (30:208), with very little selective advantage to sterility on account of self-fertilizations.

With these facts in view, we believe it reasonable to assume that between 8 and 14 approximately equal-sized intra-sterile classes or between 12 and 25 intra-sterile classes with the individuals distributed according to the point binomial coefficients, are represented in the F_2 generation,—these being taken as distributional extremes.

The second reason for approximating the number of classes is because the number of individuals investigated is comparatively small, and the probability that they are not a fair sample of the population correspondingly large.

The third reason is that the probable upper limit of the number of classes is all that is essential to our purpose. *The point is, that should the answer lie between 27 and 81 classes, the difference could be accounted for by 1 additional Mendelian factor pair.* The number of actual classes in the F_2 generation of a Mendelian population is 3^n where n represents the number of allelomorphic pairs; and 3^3 is 27, while 3^4 is 81.

Thus it is clear that with the assumptions made previously regarding the cause of self-sterility, our probable maximum cross-fertility can be interpreted by 3 (possibly 4) effective allelomorphic pairs.

For the same reasons for which it was thought best to correct the gross percentage of cross-sterility found in the F_2 generation, the later generations of this cross ought to be revised.

Considering then only the matings of the F_3 generation shown in table 5, if one counts reciprocals fertile or sterile as the case may be with the mating made, there are 98 fertile combinations and 6 sterile combinations. But mating 1×5 , made twice, yielded capsules only 30 and 35 percent full, respectively; and mating 9×3 , made thrice, yielded capsules only from 20 to 30 percent full. If, as seems probable, these are really sterile matings, the ratio of cross-sterility to the total number of cross-combinations becomes 10 to 104 or 10 percent, and the ratio of total sterility to total number of combinations becomes 22 to 116 or 19.1 percent.

Similarly correcting the results listed in table 6 for the F_4 generation, we find 16.2 percent of cross-sterility in the cross-combinations and 26.2 percent of total sterility in all combinations, with indications that plants 2, 5 and 8 belong in one class, plants 6 and 7 in a second class, and plants 9 and 10 in a third class. This result is obtained thus: there are listed 68 fertile and 6 sterile combinations, but matings 10×9 (made twice), 6×7 and 7×6 are now classed as sterile because they uniformly gave capsules less than 40 percent full.

The cross-sterility of the F_6 generation has already been analyzed sufficiently carefully in explaining table 9. Measured as above it is 22.2 percent.

Unquestionably the samples of the populations from which these results were obtained were so small and the number of matings so few,

that the probable errors are large; but rough as the determinations may be, we think that no one can question the general conclusion that in these three generations from repeated sib matings cross-sterility has increased immensely.

The cross-fertility of F_2 in this cross, as compared with the cross-fertility in those to be described next, is high. It may not be the maximum cross-fertility possible in a population from one original mating, but it is the highest found in 16 families that we have studied rather thoroughly. High as it is, nevertheless, the probable maximum number of inter-fertile, intra-sterile classes which it contains is *less than 25*, and this number may be interpreted by the permutations of 3 Mendelian allelomorphic pairs. Further the probable number of these classes in the F_5 generation can hardly be more than 8, a figure which may be interpreted by only 2 effective allelomorphic pairs. We were decidedly in error, therefore, when in 1915 we said (EAST 1915): "This is a straight mathematical problem and it is hardly necessary to say that it is insoluble by a strict Mendelian notation such as CORRENS sought to give." In justice it should be said, however, that at that time, the existence of cross-sterility in the F_2 generation was uncertain through a supposed lack of confirmatory data which was really in our possession and had been overlooked.

Cross 2. *N. alata* \times *N. Forgetiana* (*pseudo self-fertile* \times *self-sterile*)
and cross 3. *N. Forgetiana* \times *N. alata* (*self-sterile* \times *pseudo self-fertile*)

The two crosses to be described next are reciprocals made with the same two individuals. It was our intention to repeat the cross just described together with its reciprocal, and to make a more thorough study of the first hybrid generation. At the same time we intended to study the relation between self-sterility and self-fertility by crossing *N. Forgetiana* with a fertile plant of *N. alata*, since *N. alata* was then supposed to be a mixed population consisting of self-sterile and self-fertile plants. Both of these crosses were made. In crosses No. 2 and No. 3 the "self-fertile" daughter of the original supposedly self-fertile plant described on page 534 was used as the *N. alata* parent. Soon after work was started on these plants, our evidence was so conclusive that *N. alata* was always self-sterile and that this particular individual showed only pseudo-fertility caused by external conditions, that we decided to use *N. Langsdorffii* as the self-fertile strain in a series of crosses and to continue this work as a repetition of cross No. 1.

TABLE 10

Result of matings on F_1 plants 0 to 39 of cross No. 2, $N. alata \times N. Forgetiana$ and on plants 40 to 52 of cross No. 3, $N. Forgetiana \times N. alata$. Number of pollinations shown by subscripts.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
0	44, 46 ₂	22 ₂ , 34, 38 ₂ , 49
1	2, 3, 4, 6, 41	8 ₂
2	4, 18, 41, 44, 52	9, 22, 23 ₂
3	2, 9, 14, 23, 29	4 ₂ , 6 ₂ , 18 ₂ , 41 ₂ , 46
4	2 ₂ , 9, 10, 44 ₂	18
5	2, 3, 6, 9, 10 ₂ , 18 ₂ , 46	8 ₂ , 44 ₂
6	5, 10 ₂ , 43, 44	3 ₂ , 4 ₂ , 18 ₂ , 40 ₂
7	2, 13, 22, 44	18 ₂ , 46
8	6, 9, 10, 39, 40, 46 ₂	5 ₂ , 44 ₂
9	3, 18, 44, 52 ₂	24, 10, 23 ₂ , 37, 48
10	4, 6, 18, 40, 44	2 ₂ , 23, 24 ₂ , 27 ₂ , 34 ₂ , 48 ₂
11	2, 8, 12, 15, 34, 44, 46	
12	9, 16, 22, 43	6 ₂ , 18 ₂ , 46 ₂ , 52
13	3, 8, 18 ₂ , 44, 46	2, 9 ₂ , 15 ₂ , 21 ₂ , 34 ₂
14	18 ₂ , 20, 43	10, 34 ₂
15	1, 3, 16 ₂ , 17, 18, 20	9 ₂ , 13 ₂ , 14, 23 ₂ , 44
16	13, 14, 18, 25, 43 ₂ , 46	17 ₂ , 29 ₂
17	14, 18, 19, 20, 22, 30	16, 26 ₂ , 44 ₂
18	2 ₂ , 9 ₂ , 21 ₂ , 23, 28, 34, 36, 44	3, 46 ₂
19	17, 22, 28, 34, 44	18 ₂
20	2, 8 ₂ , 9, 16, 18, 20 ₂ , 21, 22 ₂ , 26, 36, 40, 44	43 ₂
21	4, 12, 16, 18, 46	2, 9 ₂ , 22 ₂ , 25, 27 ₂ , 37
22	12, 42, 44	14, 23 ₂ , 24, 36, 48 ₂
23	41	9 ₂ , 10 ₂ , 37, 48 ₂
24	3 ₂ , 6, 20, 26, 28, 44	10 ₂ , 22 ₂ , 23, 30, 37
25	8, 33, 44 ₂ , 46 ₂	2 ₂ , 9, 23 ₂ , 27
26	9, 18, 22, 23 ₂ , 25, 40, 48	28, 29 ₂ , 44 ₂
27	3 ₂ , 18, 32, 44, 46	2, 9 ₂ , 30 ₂ , 34 ₂ , 48
28	2 ₂ , 3, 23 ₂ , 27, 39, 46 ₂	8, 26 ₂ , 29 ₂ , 44 ₂
29	2, 14 ₂ , 18 ₂ , 22, 23, 24, 25, 30, 34, 37, 41, 46	5 ₂ , 26, 28, 31 ₂ , 44 ₂
30	8 ₂ , 29, 33, 44 ₂ , 45, 46	9, 21 ₂ , 22 ₂ , 27
31	22, 32, 52	8 ₂ , 29, 36, 44
32	9, 21, 23, 29, 30, 34, 43, 44	18, 33, 46 ₂
33	8, 16, 23, 31, 46	18 ₂ , 32 ₂
34	28, 41, 44, 46	10 ₂ , 23 ₂ , 24, 37 ₂
35	3, 9, 18, 21, 27, 30, 34, 37, 42	8 ₂
36	8 ₂ , 33, 44 ₂ , 46	10 ₂ , 23
37	39, 42 ₂ , 43, 44, 46 ₂	9 ₂ , 10 ₂ , 22, 23 ₂ , 34 ₂ , 38
38	28, 35, 39, 42, 43, 46 ₂	34 ₂ , 37 ₂ , 47
39	9, 44	18, 40 ₂ , 42 ₂
40	22, 43, 44, 47, 49	6, 33 ₂ , 46 ₂
41	10, 37, 44, 48	33 ₂ , 40, 46 ₂
42	20, 44	39 ₂ , 41, 45 ₂
43	5, 27, 33, 38, 39, 40 ₂ , 42, 44, 46, 51	
44	10, 14, 23, 34, 45	
45	18, 44, 48	46 ₂ , 52
46	10, 22, 37, 44, 51	52 ₂
47	20, 42, 44, 45, 46, 51, 52	38 ₂
48	40, 41, 43, 46	10, 23 ₂ , 24 ₂ , 27 ₂ , 34
49	42, 44, 45	0, 9, 27, 34 ₂ , 47
50	18, 39, 51, 52	9, 27 ₂ , 37 ₂
51	9, 18, 23, 39, 45, 46, 50	8, 29
52	10, 23, 29, 37, 51	3 ₂ , 4 ₂ , 6, 18 ₂ , 41 ₂ , 45 ₂ , 46 ₂

It is reasonable to consider these crosses in a sense to be repetitions of cross No. 1, but one must not assume that they are duplicates of cross No. 1. Both *N. alata* and *N. Forgetiana* must consist of plants which differ among themselves in the factors that affect self-sterility, hence only by following through a number of F_1 generations where these species are involved could one expect to find results duplicating those of cross No. 1. The data are none the less interesting, however, because the crosses are only similar and not identical.

The F_1 generation

All of the individuals resulting from this cross were grown in a greenhouse as potted plants. The F_1 generation came into blossom during the latter part of the winter. Conditions were extraordinarily favorable for growth and the pollinations were all made while the plants were vigorous, hence scarcely any trouble arose over classification of the results.

Our study was made on a population of 53 plants. Pedigree numbers from 0 to 39 inclusive represent cross No. 2, *N. alata* \times *N. Forgetiana*; pedigree numbers 40 to 52 inclusive represent cross No. 3, *N. Forgetiana* \times *N. alata*.

Each plant was selfed one or more times, and all proved absolutely self-sterile. Further *each plant was back-crossed with pollen from a single plant of each of the parent species with complete success in every instance.* The plants used in this work were not the individuals that entered into the cross under discussion, however, for unfortunately these were not available.

The numerous cross-pollinations made are shown in table 10. There were 103 reciprocal matings. Of these 100 gave duplicate results, 39 pairs being fertile and 61 pairs sterile. The three which did not check are:

2 \times 3,	sterile,	1 pollination	} classed as fertile
3 \times 2,	fertile,	1 pollination	
6 \times 52,	fertile,	1 pollination	} classed as sterile
52 \times 6,	sterile,	1 pollination	
37 \times 21,	fertile,	1 pollination	} classed as sterile
21 \times 37,	sterile,	1 pollination	

Since but one pollination was made in each of these cases we have made our decision as to fertility or sterility by a consideration of the circumstantial evidence. The behavior of these plants in other crosses

shows conclusively that 3 should be fertile with 2, 6 sterile with 52, and 21 sterile with 37. They have been classed accordingly. That this grouping is correct is further shown by the fact that the mating 3×2 (classed as fertile) was made at the height of the flowering season, while the matings 6×52 and 37×21 (classed as sterile) were respectively the last and next to the last matings made on those plants.

In spite of the fact that plants 0-39 are from cross No. 2, *N. alata* \times *N. Forgetiana*, and plants 40-52 are from cross No. 3, *N. Forgetiana* \times *N. alata*, they behave as one family in inter-crosses. The entire population can be grouped into 6 classes in which there is inter-class fertility and intra-class sterility (table 11). The following explanation may be necessary to make it clear just how table 11 was obtained from table 10. Table 10 shows all of the matings; but in the form given it is not easy to see at a glance every combination in which a particular plant was used, both as male and as female. It was necessary, therefore, to make a new table in which the pedigree numbers in the column at the left were tabled as males, and the pedigree numbers in the columns headed "Fertile matings" and "Sterile matings" were tabled as females. Thus plant 2 used as a female was fertile with pollen from plants 4, 18, 41, 44, and 52, and sterile with plants 9, 22 and 23; but pollen from plant 2 was fertile on plants 1, 3, 4, 5, 7, 11, 18, 20, 28 and 29, and sterile on plants 9, 10, 13, 21, 25 and 27. It is clear, therefore, that instead of the 8 matings on plant 2 that table 10 appears to show, there are really 21, the 3 reciprocals of course being counted but once.

These tables were combined for analysis. In the interest of economy only one is shown, however, since the second can easily be made from the first.

The four exceptions in this huge set of matings are in reality negligible though they are emphasized in the table by bold-faced type. Matings 15×44 and 31×36 were sterile, though they do not belong to the same class. Plant 15 was sterile to 4 plants of class A and fertile to 2 plants of class B, 3 plants of class C, and to the isolated individuals forming classes D and F. It is unquestionably a member of class A. Plant 44 was sterile to 7 individuals in class C and fertile to 17 plants of class A, 12 plants of class B and to the singletons forming classes D, E and F. This evidence places it unmistakably as a member of class C. Plant 31 is also a member of class C as evidenced by 3 sterile matings within that class and by fertile matings with 1 plant of class A and 3 plants of class B. Plant 36 is like plant 15 thrown into class A by its sterility with 3 others of that class, and by its fertility with 3 individuals

TABLE II

Plants of F₁ generation of reciprocal cross between N. Forgetiana and N. alata, grouped in accordance with their behavior in inter-crosses. Plants 0-39 are products of cross No. 2; plants 40-52 are products of reciprocal cross No. 3.

Group	Ped. No.	Number cases fertile within group						Number cases sterile within group					
		A	B	C	D	E	F	A	B	C	D	E	F
A	0	0	1	1	—	—	—	4	0	0	—	—	—
	2	0	6	5	1	—	1	8	0	0	0	—	0
	9	0	7	6	1	—	—	13	0	0	0	—	—
	10	0	7	3	—	—	—	10	0	0	—	—	—
	13	0	4	3	—	—	—	5	0	0	—	—	—
	14	0	2	4	1	1	—	4	0	0	0	0	—
	15	0	2	3	1	—	1	4	0	1	0	—	0
	21	0	5	2	1	—	—	8	0	0	0	—	—
	22	0	6	5	1	—	—	9	0	0	0	—	—
	23	0	6	5	—	—	—	11	0	0	—	—	—
	24	0	2	4	1	—	—	7	0	0	0	—	—
	25	0	2	5	—	—	—	5	0	0	—	—	—
	27	0	4	3	—	1	—	10	0	0	—	0	—
	30	0	4	5	—	—	—	5	0	0	—	—	—
	34	0	5	4	—	—	1	11	0	0	—	—	0
	36	0	3	2	1	—	—	3	0	1	0	—	—
	37	0	5	3	—	1	—	9	0	0	—	0	—
	38	0	3	2	—	1	—	4	0	0	—	0	—
	47	0	5	2	1	—	—	2	0	0	0	—	—
	48	0	4	1	—	1	—	7	0	0	—	0	—
	49	0	3	1	—	—	—	5	0	0	—	—	—
	50	0	3	1	—	—	—	3	0	0	—	—	—
B	3	8	0	5	—	—	—	0	6	0	—	—	—
	4	4	0	2	—	—	—	0	4	0	—	—	—
	6	2	0	4	—	1	—	0	6	0	—	0	—
	7	3	0	1	—	—	—	0	2	0	—	—	—
	12	3	0	1	—	1	1	0	4	0	—	0	0
	18	12	1	9	1	—	—	0	11	0	0	—	—
	19	2	0	3	—	—	—	0	1	0	—	—	—
	32	6	0	3	—	1	—	0	3	0	—	0	—
	33	4	1	3	0	1	—	0	4	0	—	0	—
	39	4	0	4	—	1	—	0	3	0	—	0	—
	40	5	0	3	1	1	—	0	5	0	0	0	—
	41	6	0	3	—	—	—	0	6	0	—	—	—
	42	5	0	2	1	1	—	0	3	0	0	0	—
	45	4	1	2	—	—	—	0	3	0	—	—	—
	46	14	1	7	—	1	1	0	9	0	—	0	0
	52	7	0	3	—	—	—	0	8	0	—	—	—
C	1	2	4	0	—	—	—	0	0	1	—	—	—
	5	3	4	0	—	1	—	0	0	3	—	0	—
	8	6	5	0	1	—	1	0	0	7	0	—	0
	16	5	4	0	1	1	—	0	0	2	0	0	—
	17	4	2	0	1	—	—	0	0	3	0	—	—
	26	6	2	0	1	—	—	0	0	4	0	—	—
	28	6	5	0	—	—	—	0	0	4	—	—	—
	29	9	6	0	—	—	—	0	0	7	—	—	—
	31	1	3	0	—	—	—	1	0	3	—	—	—
	35	7	3	0	—	—	—	0	0	1	—	—	—
	44	17	12	0	1	1	1	1	0	7	0	0	0
	51	4	5	0	—	1	—	0	0	2	—	0	—
D	20	9	3	5	—	1	—	0	0	0	—	0	—
E	43	5	8	4	1	—	—	0	0	0	0	—	—
F	11	3	2	2	—	—	—	0	0	0	—	—	—

of class B, with 2 of class C, and with the lone plant of class D. In view of this evidence and the fact that in these two matings but one pollination was made in each case, they are much more likely to be errors of record or of technique than true exceptions to our classification.

The other two exceptions, matings 45×18 and 33×46 , were fertile where from the evidence of numerous other matings they should have been sterile. Here again but one pollination was made in each case; and, coincidence though it may be, *each pollination was the last mating made on that particular plant*. What is more probable than that this is a pseudo fertility appearing during the wane of the flowering season of the two mother plants, No. 45 and No. 33?

Six groups appear in table 11, but there is proof of the existence of only five. Groups A, B, C, D and E are definitely established. Plant 11, on the other hand, is an isolated individual rather than a class. It does not belong to groups A, B, or C; but unfortunately it was not crossed either with class D (plant 20) or with class E (plant 43), hence one cannot say that it does not fall into one or the other of these two classes.

In the three large groups the distribution of individuals is 22, 16 and 12. About all that can be said about the type of this distribution is that the classes appear not to be of equal size. On the other hand, it is interesting to note that the plants of both cross No. 2 and cross No. 3 fell into the three groups as if they were samples of the same population. There were 40 plants of cross No. 1, and 12 plants of the reciprocal cross No. 2. In the classes A, B and C the proportions were 18, 10, 10 and 4, 6, 2, respectively. This similar behavior of the progeny of reciprocals seems to us strong corroboratory evidence in favor of the conclusion that reciprocal crosses always behave in like manner as regards self-sterility.

It is interesting here to check our *a posteriori* probabilities with the facts. There were 278 fertile matings made in this family, of which 39 were reciprocals, making 478 ($278 \times 2 - 78$) fertile combinations altogether. There were 167 sterile matings, of which 61 were reciprocals, making a total of 212 ($167 \times 2 - 122$) cross-sterile combinations. If to the cross-sterile combinations, the 53 self-sterile combinations be added, there is a total of 265 sterile combinations out of 743,—a percentage of 35.6 ± 1.2 . Assuming a point binomial distribution of individuals we should expect 4 intra-sterile classes for this percentage of sterility; but since we must discount the selection of self-combinations a little, perhaps 5 classes may be taken as the probable expectancy.

It was planned to continue the study of this family—considering it as a single cross—on populations obtained by back-crossing a representative of each of the large classes A, B, and C with both parents, and by intercrossing the same three individuals among themselves. This rather Herculean task has not been finished. The progeny of a part of these matings was investigated as thoroughly as time permitted in 1915-16, but much remains to be done. These families came from the following combinations:

Family D, *N. alata* plant 53 \times plant 44 of class C

Family E, *N. alata* plant 58 \times plant 44 of class C

Family F, plant 34 of class A \times *N. Forgetiana*

Family G, plant 44 of class C \times *N. Forgetiana*

Family H, plant 44 of class C \times plant 10 of class A

Family I, plant 44 of class C \times plant 34 of class A

Family J, plant 52 of class B \times plant 23 of class A

Family K, plant 52 of class B \times plant 44 of class C

In families D and E we have two *N. alata* plants 53 and 58 crossed with the same plant of cross 3 (table 11), No. 44 a member of class C. Families F and G were produced by crossing individuals of classes A (34) and C (44) with the same plant of the other parent species *N. Forgetiana*. The four remaining families are true F_2 generations formed by mating two F_1 plants. There is a duplicate test of plant 44 (class C) with two plants of class A, 10 and 34. Then there is a test of plant 52 (class B) with plant 23 of class A and plant 44 of class C. Thus plant 44 of class C enters into two back-crosses with *N. alata*, one back-cross with *N. Forgetiana*, and matings with two individuals belonging to class A and one individual belonging to class B.

Family D,—*N. alata* plant 53 \times plant 44 of class C, cross No. 3

The first of the eight F_2 populations of crosses No. 2 and No. 3 was produced by back-crossing. Plant 53 of *N. alata* (table 1), a plant apparently¹⁵ fertile with sister plants 57 and 58, and sterile with sister plants 54, 56 and 59, was crossed with the pollen of plant 44 of class C, cross 3. In a manner of speaking, it may be called $P_1 \times F_1$, if it be remembered that plant 53 is not the same plant of *N. alata* used in making cross No. 3.

Table 12 shows the self-pollinations made on 39 plants. They behaved in much the same manner as the *N. alata* plants recorded in tables 1-3. One-third of them produced some seed, though from 1 to 10 failures

¹⁵ See page 533.

TABLE 12

Family D.—Record of self-pollinations on progeny of N. alata plant 53 × plant 44 of F₁ of cross No. 3

Ped. No.	No. selfings sterile	No. of selfings giving capsules with		
		1-10 seeds	10-50 seeds	250-300 seeds
151	11			
152	15			
153	6			
154	10			
155	14			
156	10	1		
157	1			
158	4			
159	2			
160	2			1
161	1			
162	8			
163	3			
164	7			
165	3	2		6
166	10	2		
167	7			
168	1			
169	1			
170	9			
171	5		2	
172	1			
173	2			
174	10			
175	1			1
176	3			
177	10	2		
178	11		5	
179	5			
180	4			
181	5			
182	8		1	
183	5		1	
184	3			
185	1	4		
186	6		1	
187	8	4		
188	16			
189	9			

were also recorded for the same plants. The remaining plants produced no capsules. There was an extremely high correlation between this partial fertility which we have regarded as false, and the close of the reproductive period. Yet one cannot say that every plant can be made to produce seeds at this phase of the life cycle, even under adverse conditions. This may be the case, but we have been unable to demonstrate it. 4 plants in this family, however, gave a very nice demonstration of the fact

that complete self-sterility returns with the return of a new flowering season. A number of these plants were selfed at various times during two flowering periods, and plants 156, 166, 177 and 178, though giving a

TABLE 13

Family D.—Record of cross-pollinations on progeny of N. alata plant 53 × plant 44 of F₁ of cross No. 3 outside of family D.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
152		204 Family E
153		204 Family E
167	201 Family E	
171	201 Family E	
174	58 <i>N. alata</i>	

TABLE 14

Family D.—Record of cross-pollinations on progeny of N. alata plant 53 × plant 44 of F₁ of cross No. 3.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
151	159	
152	160	185
153		152
154	151	153
155		154
157	154	
159		
160		174
161		162
162		163, 168
163	185	
168	173	
170	168	
172	175	
173	159,	
174		
175		185
177	168, 182,	183
179	177	
180	177	
181		183
182	160, 183	185
183		177
184	185	188
185	160, 174	
186	185	160?
187		185
188	185	

few poor capsules at the end of the first flowering season, showed complete self-sterility from the beginning to the height of the second flowering period. Then, in two cases, the slight degree of fertility shown at the end of the first flowering season returned. 3 plants produced full capsules. No. 160 and No. 175 yielded 1 each, both according to the late

TABLE 15

Family D.—Progeny of N. alata plant 53 × plant 44 of F₁ of cross No. 3 grouped in accordance with their behavior in inter-crosses.

Group	No. Ped.	No. cases fertile within group						No. cases sterile within group					
		A	B	C	D	E	Ind.	A	B	C	D	E	Ind.
A	152	0	1	—	—	—	—	2	0	—	—	—	—
	153	0	—	—	—	—	—	2	—	—	—	—	—
	154	0	—	—	—	—	2	2	—	—	—	—	0
	155	0	—	—	—	—	—	1	—	—	—	—	—
	175	0	—	—	—	—	1	1	—	—	—	—	0
	182	0	1	—	2	—	—	1	0	—	0	—	—
	185	0	3	1	—	2	—	4	0	0	—	0	—
	187	0	—	—	—	—	—	1	—	—	—	—	—
B	160	3	0	—	—	—	—	0	2	—	—	—	—
	174	1	0	—	—	—	—	0	1	—	—	—	—
	186	1	0	—	—	—	—	0	1	—	—	—	—
C	161	—	—	0	—	—	—	—	—	1	—	—	—
	162	—	—	0	—	—	—	—	—	3	—	—	—
	163	1	—	0	—	—	—	0	—	1	—	—	—
	168	—	—	0	1	—	2	—	—	1	0	—	—
D	177	1	—	1	0	—	2	0	—	0	1	—	0
	181	—	—	—	0	—	—	—	—	—	1	—	—
	183	1	—	—	0	—	—	0	—	—	2	—	—
E	184	1	—	—	—	0	—	0	—	—	—	1	—
	188	1	—	—	—	0	—	0	—	—	—	1	—

TABLE 16

Family E.—Record of cross-pollinations on progeny of N. alata plant 58 × plant 44 of F₁ of cross No. 3.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
191		197
192		191
193		44 ₁ , 58 ₁
194		58 ₂
195		193, 204
197		199
199		195
200		204
202		197
204		152 Family D
205		204

season expectation. No. 165, on the other hand, was somewhat of an exception to the usual rule, in that it produced 6 full capsules out of 11 pollinations. There were 2 failures and 2 small capsules with from 1-10 seeds each from pollinations made during the height of the flowering season. Toward the end of the flowering period the plant was tested again and yielded 6 good capsules out of 7 flowers selfed.

Five plants of family D were crossed with individuals outside of that group, as is shown in table 13. 2 plants, 167 and 171, were fertile with the pollen of plant 201 of family E, while 2 other plants, 152 and 153, were sterile to the pollen of plant 204 of family E. Plant 174 was fertile with *N. alata* plant 58.

Only 36 cross-matings were made between plants of this family (table 14). Of these, 16 were failures. In spite of this small number of intercrosses, 20 out of 28 plants can be shown to belong to not over 5 classes wherein the plants are intra-class sterile and inter-class fertile (table 15). The other 8 plants show only 1 or 2 cases of cross-fertility and no cross-sterility, and may or may not belong to separate groups. Their fertility with the other classes is shown in the column marked "Indeterminate."

There are no exceptions in table 15. Each plant in every group is wholly intra-class sterile and inter-class fertile as far as it was tested. But these five groups are not necessarily independent. A is not B, C, D, E, 151, 157, or 172; B is not A; C is not A, D, 170 or 173; and D is not A, C, 179 or 180. Therefore B may be C, etc., and the existence of only three groups is demonstrated.

An estimation of the number of classes by formula is hardly desirable on account of the small number of combinations made per plant, though the total number of combinations is larger than appears at first sight because only 1 reciprocal (sterile) was made. There are really 70 combinations of which 30 are sterile, a cross-sterility percentage of 42.8.

Family E.—*N. alata* plant 58 \times plant 44 of class C of cross No. 3

Family E resulted from a cross between *N. alata* plant 58 and plant 44 of class C, cross No. 3. The interesting thing about the family is its lack of fertility not only when selfed but also in crosses. 10 plants were mated together in such a manner that the chain of evidence was not broken, as can be seen by studying table 16, with no evidence whatever of any fertility between them. *They all belong to one class showing perfect intra-class sterility.* In addition, if one may assume that all of the individuals would have behaved as plants 193 and 194, the group was sterile to the 2 parents. Plant 204 was also sterile reciprocally with plant

152 of family D, and as a male with plant 153 of family D. The only sign of cross-fertility shown was when pollen from plant 201 (which also belonged to family E) was used on plants 167 and 171 of family D, yet in appearance the pollen of these plants was perfectly good.

It is unfortunate that the behavior of more plants of this family was not investigated, but a good many plants needed attention at the same time during the period these were in flower, and the importance of establishing definitely whether the entire family belonged to one class was overlooked until too late. It is clear, however, that if other classes existed, they must have contained relatively fewer individuals than the one found.

Judged by its parents family E appears to be a duplicate of family D. *N. alata* plant 58 was apparently fertile to its sister plants 53 and 59, and sterile to its sister plants 54, 56, 57, 62, 64, 66, 71 and 79; plant 53, the female parent of family D, was apparently fertile to plants 57 and 58,

TABLE 17

Family F.—Record of self-pollinations on progeny of plant 34 of F, of cross No. 2 \times plant A.1 of *N. Forgetiana*.

Ped. No.	No. selfings sterile	No. of selfings giving capsules with		
		1-10 seeds	10-50 seeds	250-300 seeds
207	9			
211	8			
212	4			
214	11			
215	1			
216	22			
217	12			
218	8			
219	5			
225	11	I		
227	3			
228	12			
229	1			
230	10			
231	10			
232	9			
233	1			
234	1			
235	5			
236	6	I		
237	6			
239	9			
240	11			
241	1			
242	12		I	
243	18			
244	1			

and sterile to plants 54, 56 and 59 of the same family. But considering the behavior of *N. alata* plants 53-79 of table 1 as a whole there is good reason to believe that they all belong to 1 intra-sterile class and that the fertility of matings 53×57 , 58×53 and 58×59 is pseudo-fertility. For this reason one might expect family D and family E to behave similarly; but unless one assumes the existence of other classes of low frequency in family E, their behavior was different.

Family F.—Plant 34 of class A \times plant AA of *N. Forgetiana*

Family F resulted from crossing plant 34 of class A, cross No. 2, with a plant of *N. Forgetiana*; but, as in families D and E, it was not a true back-cross, since the plant of *N. Forgetiana* used was not the individual that participated in the original mating.

Selfings were made on 27 hothouse-grown plants with the results shown in table 17. It will be noticed that only 3 individuals produced any seeds at all. No. 225 yielded 1 capsule containing 8 seeds in 12 tests; No. 236 produced 1 capsule containing 7 seeds in 7 trials; and No. 241 finally produced a single capsule having about 30 seeds after 12 pollinations. This is a considerably smaller seed production than was recorded for family D, and we believe it to be due to the fact that family F came into blossom somewhat later than family D, thus making it practicable to conclude the pollinations during the height of the flowering season.

A few pollinations were made between plants of this family and plants of family G, the results of which are set forth in table 18. They will be discussed when describing that family.

We were able to make 151 cross-matings on this family, with the results shown in table 19. Some of these matings, unlike the self-pollinations were made rather late in the flowering season. These made trouble in some cases, and had to be repeated several times before a proper decision as to fertility or sterility could be made. In all there were 17 matings that gave seeds in some tests and none in other trials. If the capsules were full and the majority of pollinations succeeded, the mating was called fertile; if the capsules were small and poorly filled, and the majority of the pollinations failed completely, the mating was called sterile.

These 17 matings, we believe, are listed correctly, but there are a few matings made but once during the latter part of the season which may be recorded erroneously.

In addition, plant No. 225 had poor pollen and decision as to the

TABLE 18

Family F.—Record of cross-pollinations on progeny of plant 34 of F_1 of cross No. 2 \times plant AA of *N. Forgetiana* outside of family F.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
216	278 fam. G.	247 fam. G.
219		250 fam. G.
239		247 fam. G.
241		
243	250 fam. G.	
244	247 fam. G.	247 fam. G.

TABLE 19

Family F.—Record of cross-pollinations on progeny of plant 34 of F_1 of cross No. 2 \times plant AA of *N. Forgetiana*.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
207	211, 216, 225	
209	212, 216, 231	
211	209 ₃ , 214, 216	212 ₂ , 215
212	214 ₂ , 216 ₁ , 231	
214	209, 211, 216 ₂ , 217, 219, 228	
215	214, 217 ₂ , 219, 222	
216	212, 217 ₃ , 219 ₂ , 223	239
217	216 ₂ , 218, 219 ₂	212
218	217, 219	
219	214 ₂ , 215, 216, 217 ₁ , 218 ₂ , 227	228
221	227	
222	217 ₂ , 218, 219 ₂	
223	216, 225 ₃ , 227, 228, 230, 236	
224	217, 219, 223, 225 ₂	
225	216, 217 ₂ , 219, 221, 223, 228, 230 ₁ , 234 ₂ , 235	
226	227 ₂ , 228, 230, 234 ₃	223
227	219 ₂ , 224, 225 ₃	
228	222, 223 ₂ , 225 ₂ , 227, 230	219
229	209, 214, 216, 219, 231 ₁	
230	223, 225 ₂ , 227, 234, 236	
231	212, 214, 219, 229 ₅	
232	236, 239 ₂ , 243	219, 234
233	223, 234, 239	
234	225, 226, 230 ₃ , 239 ₃	219, 228, 232 ₁
235	236 ₂ , 239	232
236	232, 234 ₂ , 239 ₂ , 243	233
237		235 ₁
238	239, 243 ₂ , 244 ₂	
239	219, 232, 235, 236, 240	243 ₂
240	234, 236, 239, 243	
241	234 ₂ , 236, 244 ₃	
242		239, 243 ₃
243	234, 244 ₂	239, 243 ₂
244	236, 238 ₂ , 239 ₂ , 241 ₂ , 243 ₂	239 ₁ , 241, 242
245	238 ₂ , 241 ₂ , 243, 244	

character of three matings (with 219, 227 and 230) was made on the basis of the successes obtained when No. 225 was used as female.

There were 23 unsuccessful and 128 successful cross-matings in this family. Of these combinations, 55 were reciprocals fertile in both matings and 10 were reciprocals sterile both ways.

Eighteen of the plants can be grouped into 6 inter-class fertile, intra-class sterile groups of 2 or more plants each (table 20), but these groups are not necessarily independent. A is not B, C, D or F; B is not A, C, D, E or F; C is not A or B; B is not A, B or F; E is not B or F; and F is not A, B, D or E. Therefore, C may be D, E or F; D may be C or E; E may be C or D; and F may be C. But since 2 of these alternatives are mutually exclusive, it is definitely established that at least 4 of these groups are independent of each other.

This matter is shown more clearly in table 21, where the 17 other plants which exhibited no cross-sterility are also listed. From this table by the process of elimination cited above it can be shown that 5 separate inter-class fertile, intra-class sterile groups must exist. Since there are 16 plants unplaced because they have had only a few cross-matings made upon them, however, it may be well to compare the number of classes proved with the number to be expected from the percentage of sterility

TABLE 20

Family F.—Progeny of plant 34 of F, of cross No. 2 × plant AA of N. Forgetiana grouped in accordance with their behavior in inter-crosses.

Group	Ped. No.	No. cases fertile within group						No. cases sterile within group					
		A	B	C	D	E	F	A	B	C	D	E	F
A	219	0	2	1	—	—	—	3	0	0	—	—	—
	228	0	—	—	2	—	—	2	—	—	0	—	—
	232	0	2	—	—	0	1	2	0	—	—	1	0
	234	0	3	—	1	—	2	3	0	—	0	—	0
B	216	1	0	2	1	—	—	0	1	0	0	—	—
	239	3	0	—	—	1	2	0	4	—	—	0	0
	241	1	0	—	—	—	1	0	2	—	—	—	0
	242	—	0	—	—	—	—	—	2	—	—	—	—
	243	2	0	—	—	—	1	0	3	—	—	—	0
C	211	—	1	0	—	—	—	—	0	2	—	—	—
	212	—	1	0	—	—	—	—	0	1	—	—	—
	215	1	1	0	—	—	—	0	0	1	—	—	—
D	223	1	1	—	0	—	2	0	0	—	1	—	0
	226	2	—	—	0	—	—	0	—	—	1	—	—
E	235	0	1	—	—	0	1	1	0	—	—	1	0
	237	—	—	—	—	0	—	—	—	—	—	1	—
F	233	1	1	—	1	—	0	0	0	—	0	—	1
	236	2	3	—	1	1	0	0	0	—	0	0	1

found, on the theory of a distribution of individuals corresponding to the frequencies of the coefficients of the binomial expansion. In family F there are 128 fertile matings, of which 55 are reciprocals, a total of 146 ($128 \times 2 - 110$) fertile combinations. Likewise there are 23 sterile matings, of which 10 are reciprocals, a total of 26 ($23 \times 2 - 20$) sterile combinations. This amounts to a cross-sterility of 15.1 percent. Adding the 35 self-combinations to the steriles, gives 61 cases of sterility out of 207 combinations,—a percentage of 29.4. We should expect only about 5 intra-sterile classes in this population, therefore, unless a very broad allowance is made for *selection* of matings that were sterile.'

TABLE 22

Family G.—Record of cross-pollinations on progeny of plant 44 of F₁ of cross No. 3 \times plant AA of N. Forgetiana outside of family G.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
247	44 ♀ parent, F ₁ plant	
249	44 ♀ parent, 351 ₃ , fam. H, 467 ₃ , fam. I	
258	34 ₂ F ₁ plant	
278	219 fam. F, 374 fam. H, 467 fam. I	
281	405 ₂ fam. I	
293	44 ♀ parent, F ₁ plant	
308	34 ₂ F ₁ plant	

Family G.—Plant 44 of class C, cross No. 3 \times plant AA of *N. Forgetiana*.

Family G was produced by mating plant 44 of class C, cross No. 3, with the same plant of *N. Forgetiana* used in producing family F. In all, 53 hothouse-grown plants had some work done upon them, although in a few cases only one mating was made. These plants were studied during a complete flowering season, but nearly all of the work was completed before the period of decline in reproductive vigor so that only a few cases of pseudo-fertility were found. 31 of the plants were selfed from 1 to 19 times with the production of a few seeds in one attempt at selfing only (308). In 12 other matings there was some conflict in the results. These were classified, as before, by recording as fertile those that gave full capsules in two or more trials even though one trial failed, or by recording as sterile those in which a majority of the trials failed even though a portion of the pollinations did produce a few seeds (less than 15 percent of normal).

Table 22 records the crosses made when plants outside of family G

TABLE 23

Family G.—Record of cross-pollinations on progeny of plant 44 of F_1 of cross No. 3 \times plant AA of N. Forgetiana.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
247	248 ₁ , 250 ₁ , 253 ₁ , 256, 263, 276	
248	247	
249	247 ₂ , 250 ₂ , 256	
250	247 ₁ , 249	253
251	270	
252	247 ₂ , 249, 256, 257	250, 255
253	247 ₂ , 256, 262	255
255	249, 262	252
256	253	
257	255, 256 ₂	
258	247, 257, 269	270 ₂
259	258 ₂ , 262	
260	251 ₂ , 255, 262	
262	266, 271	
263	250, 253	258 ₂
265	263, 266, 269, 276 ₂ , 278	
266	263, 265, 270 ₂ , 281	
267	251	
268	284	289
269	270, 281	
270		260
271	274	
272	255, 256, 270, 281	
273	275, 276, 281	
274	269, 275 ₂	270 ₂
275	258, 270 ₂ , 274, 278	
276	270, 275, 281	
278	269, 274, 285, 289	281 ₂ , 284 ₁
279	289	281
281	276 ₁ , 284	275, 278
283	270	276
284	281, 285, 289	
285	289, 293, 306, 309	304 ₂
286	278, 284	289
288		289
289	265, 269, 284, 293 ₂	286, 306
290	258, 278, 289	
291		284
293	274, 285 ₂ , 289, 290	284
295	310	
297	289	
298	284 ₂	
303	285 ₂ , 304, 306 ₂	
304	293, 306 ₂ , 309, 310	307
305	312	311
306	284, 293, 304 ₁ , 309, 310	289
307	310	304
308	312	
309	304 ₁ , 310 ₂ , 311	308
310	304, 308, 309 ₂ , 311, 312	
311	308 ₂ , 309 ₂ , 310 ₂	
312	309, 310 ₂	311 ₂

were used as pollen parents. The 11 matings tried were all successful. 3 back-crosses were made with plant 44, 2 with plant 34 of F_1 , 2 with plants of family H and 3 with plants of family I. It should be noted, however, that of 7 crosses of plants of family F with pollen from individuals of family G, 4 were failures. On the other hand, G family pollen was fertile on 3 plants of family H (table 27) and on 1 plant of family I (table 30).

Table 23 shows the cross-matings made within family G. There were 126 successful matings,—19 being pairs of reciprocals,—making 214 successful combinations. 29 matings were sterile, including 5 pairs of reciprocals,—48 combinations in all. 314 combinations have been made, therefore, 100 being sterile (52 selfs + 48 crosses) and 214 fertile. The probable sterility is thus 31.2 percent \pm 1.8 percent.

Table 24 shows 27 plants of this family grouped in accordance with

TABLE 24

Family G.—Progeny of plant 44 of cross No. 3 \times plant AA of N. Forgetiana grouped in accordance with their behavior in inter-crosses.

Group	Ped. No.	No. cases fertile within group						No. cases sterile within group					
		A	B	C	D	E	F	A	B	C	D	E	F
A	250	0	1	—	—	—	—	2	0	—	—	—	—
	252	0	—	—	—	—	—	2	—	—	—	—	—
	253	0	1	—	—	—	—	2	0	—	—	—	—
	255	0	1	—	—	—	—	2	0	—	—	—	—
B	258	—	0	1	—	—	—	—	2	0	—	—	—
	260	1	0	—	—	—	—	0	1	—	—	—	—
	263	2	0	—	—	—	—	0	1	—	—	—	—
	270	—	0	1	—	—	—	—	3	0	—	—	—
	274	—	0	3	—	—	—	—	1	0	—	—	—
C	275	—	3	1	—	—	—	—	0	1	—	—	—
	278	—	1	1	2	1	—	—	0	2	0	0	—
	279	—	—	0	1	—	—	—	—	1	0	—	—
	281	—	—	1	—	—	—	—	—	3	—	—	—
	284	—	—	1	4	—	—	—	—	3	0	—	—
	291	—	—	0	—	—	—	—	—	1	—	—	—
D	293	—	1	0	2	2	—	—	0	1	0	0	—
	268	—	—	1	0	—	—	—	—	0	1	—	—
	286	—	—	2	0	—	—	—	—	0	1	—	—
	288	—	—	—	0	—	—	—	—	—	1	—	—
	289	—	—	4	0	1	—	—	—	0	4	0	—
E	306	—	—	2	0	2	—	—	—	0	1	0	—
	285	—	—	3	2	0	—	—	—	0	0	1	—
	304	—	—	1	1	0	—	—	—	0	0	2	—
	307	—	—	—	—	0	—	—	—	—	—	1	—
F	305	—	—	—	—	—	1	—	—	—	—	—	1
	311	—	—	—	—	—	0	—	—	—	—	—	2
	312	—	—	—	—	—	1	—	—	—	—	—	1

their behavior in inter-crosses. There are 6 classes as tabled with a frequency of 3, 5, 7, 5, 4, 3. There are 3 exceptions among the fertile matings, 275×278 , 281×284 and 305×312 . Only one pollination each was made on the first and third of these combinations, but the second was made reciprocally—the last of the flowering season—one pollination each way. *There were no sterile exceptions.*

Though 6 intra-sterile groups are tabled, there is definite proof of the existence of only 3 classes. This is easily seen by referring to the table. Classes C, D and E must be different, but the other 3 groups might have proved to fall in with them had the proper crosses been made. Nor can the existence of more than 4 intra-class sterile groups be proved even by the complete table of inter-class fertility shown as table 25. By our probability formula also the presumption is that there are but 4 or 5 classes, whether the distribution of individuals be according to the coefficients of the binomial expansion or into classes of equal size.

Family H.—Plant 44 of class C, cross No. 3 \times plant 10 of class A, cross No. 2.

Family H was one of the 30 true F_2 populations possible from combinations of the 6 different F_1 classes. It was produced by crossing plant 44 of class C, cross No. 3 with pollen from plant 10 of class A, cross No. 2. 70 plants were grown in the greenhouse. Self-pollinations were made on 33 of these individuals with the results listed in table 26. In view of previous results it seemed hardly necessary to self every member of the population. If this had been done a truly self-fertile plant might have been discovered, of course, but it is exceedingly improbable. Of those selfed, 5 did produce some seed,—the amounts being shown in the table. These capsules were all produced at the very end of the flowering season, except 1 with 8 seeds in it on plant 316. There is a chance that these seeds were produced by foreign pollen, though it is hardly necessary to "explain" such a rare exception to the general rule.

This family was studied through a long flowering season. Many matings were made, and the work completed before we were certain of the effects of environment on self-sterility. For this reason some of the matings made toward the end of the season were not tested as thoroughly as should have been done. Further, no records of the number of seeds were taken in the case of several capsules that were not full. Thus it is altogether likely that several matings marked fertile were in reality sterile. The maximum number of such errors, we should judge from a careful examination of our records ought not to be over 10.

It is also probable that the usual experimental error of 4 failures per hundred in actually fertile matings obtains in cases where a mating was made but once and proved sterile. There were 63 such matings in the intra-family crosses, thereby making 3 such errors probable. The remaining combinations were judged by several matings and by reciprocal crosses, and are likely to be correct.

It is clear that the errors mentioned above are largely compensatory when figuring the percentages of fertility or sterility in the matings made, but they will stand revealed when endeavoring to group the individuals in intra-sterile classes.

The record of back-crosses and crosses made with plants outside of

TABLE 26

Family H.—Record of self-pollinations on progeny of plant 44 (F_1 , cross No. 3, class C) \times plant 10 (F_1 , cross No. 2, class A).

Ped. No.	No. selfings sterile	No. of selfings giving capsules with			
		1-10 seeds	10-50 seeds	50-150 seeds	250-300 seeds
314	1				
315	4		2	2	
316	9	1	3		
317	4				
318	3				
321	1				
324	1				
330	1				
331	2				
332	6				
333	1				
334	1				
335	3				2
336	1				
340	1				
342	3				
347	1				
350	3		1		
351	1				
353	1				
354	10				
358	9		1		
362	4				
363	7				
368	4				
370	1				
371	3				
373	4				
374	2				
378	1				
381	2				
382	2				
385	1				

TABLE 27

Family H.—Record of cross-pollinations on progeny of plant 44 (F_1 , cross No. 2, class C) \times plant 10 (F_1 , cross No. 2, class A) outside family H.

Fed. No. ♀	Fertile with parents ♂	Sterile with parents ♂	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
314	44, 10 ₂			
315	44 ₂			
317	44 ₂	10 ₁	311 fam. G	34 ₂ F ₁
318		10		
319		10 ₁	311 fam. G	
320	10 ₁			
321		10 ₁	311 fam. G	
322		10 ₂		
324		10		
327	44 ₁	10 ₂		
328	44 ₂			
329	44 ₃			
330		10 ₁		
331	44 ₁	10		
334		10		
335	44 ₁ , 10	10		
337		10	477 fam. J, 524 fam K	
339				18 F ₁
340		10		
342	44 ₂ , 10 poor	10 ₂		467 fam. I
349		10		
350	44	10 ₂		
351		10		
354	44 ₁	10 ₁	467 fam. I	34 ₁ F ₁ , 401 fam. I
362	10, 8 seeds	10 ₁		34 ₂ F ₁
363	44	10 ₁		
365	44			
366		44		
367	10	10		
368	10 ₁		467 fam. I	
371	44		467 fam. I	
373	44 ₁ , 10			
374	44 ₁			401 fam. I, 467 ₂ fam. I
378	44			
379	44 ₁	10 ₂		
381	44, 10		405 fam. I, 415 fam. I	
382	44 ₁ , 10 ₂			
384	44			
385	44 ₂	10		

family H, are shown in table 27, but they can be discussed best after dealing with the intra-family matings.

Excluding selfings, 312 intra-family matings were made on 56 plants. If we take all of these plants to be self-sterile,—a reasonable assumption even though a few of them were not selfed—448 combinations out of a possible 3136 were attempted. The figure 448 is the sum $153 \times 2 = 306$ fertile matings, minus 100, the number of fertile reciprocals, plus $159 \times 2 = 318$ sterile matings, minus 132, the number of

TABLE 28

Family H.—Record of cross-pollinations on progeny of plant 41 (F₁, cross No. 2, class C) × plant 10 (F₁, cross No. 2, class A).

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
315		316, 317, 318 ₂
316	320, 324	317 ₂ , 318, 321, 331
317	320	315 ₂ , 318, 321, 327 ₂ , 328 ₂
318	320 ₂ , 328	315 ₂ , 316, 317 ₂ , 321 ₂ , 324
319	347	315, 316, 317 ₂ , 354 ₂ , 381
320	317, 318, 321, 322, 324 ₂ , 328 ₂ , 354 ₂ , 381	342, 351
321	320 ₂ , 335 ₂ , 381	315 ₂ , 316 ₂ , 322 ₂ , 328 ₂
322	320 ₂ , 325, 381 ₂	321, 324, 328, 329
324	320 ₂ , 325, 342, 367 ₂ , 379 ₂	322, 327, 328, 331, 354 ₂
325	317, 322 ₂ , 324, 329	
327	351	330, 336 ₂ , 337 ₂ , 340 ₂ , 345
328	335, 337	317, 324, 327, 329, 342
329	325, 347	324 ₂ , 327, 328
330	335	327, 334, 374
331	335 ₂	316 ₂ , 327, 328 ₂ , 329, 330, 336
333	336 ₂	
334	335	331 ₂ , 337, 374
335	321, 324, 327, 328, 329, 331	320, 336, 381 ₂
336	328, 351 ₂	327 ₂ , 331, 337 ₂ , 342, 345
337	339	327, 336, 340 ₂
338	327, 337, 341, 342	
339	318, 327, 336, 337 ₂ , 340, 342 ₂	338
340		327, 337 ₂ , 342 ₂ , 345, 346
341	327 ₂ , 331, 337 ₂ , 340 ₂ , 342 ₂	
342	347 ₂ , 351, 373 ₂ , 381	336, 340, 345, 354 ₂ , 371, 374
345		327, 337 ₂ , 342
347	337 ₂ , 340, 342, 349 ₂ , 354	
348	342, 347	351
349	351 ₂	342 ₂
350	381 ₂	334, 337, 340, 349, 354 ₂ , 359, 363
351	349 ₂ , 350, 353, 354 ₂ , 362	320, 368, 381 ₂
352	327, 342, 349 ₂	348
353	351 ₂	354 ₂ , 362 ₂
354	351 ₂ , 371	317 ₂ , 337, 350, 363 ₂ , 374 ₂
355	342 ₂ , 351, 354 ₂ , 381	
358		354 ₂ , 362
359	347, 351, 355 ₂ , 366 ₂	342, 354 ₂ , 362, 371 ₂
360		362, 363 ₂
362	368, 381 ₂	340, 354, 358, 363, 365
363	351, 366, 368 ₂	350 ₂ , 354, 365
365	355, 368	354, 359, 362, 363, 374
366	351, 354 ₂ , 360, 363, 365, 368 ₂	
367	354 ₂ , 370 ₂ , 371	378
368	354, 363, 371, 374	320 ₂ , 367, 381 ₂
370	367 ₂ , 368 ₂ , 373, 378	371, 372, 374
371	366, 368, 381 ₂	365 ₂ , 374 ₂
372	367 ₂ , 368, 381	371 ₂ , 374
373	354 ₂ , 367, 370 ₂ , 374 ₂ , 385, 371 ₂	320 ₂ , 368, 381
374	373, 378, 381	371 ₂
378	373, 381 ₂ , 383	379 ₂
379	374 ₂ , 381 ₂ , 383	354 ₂ , 373 ₂
381	317 ₂ , 340, 341, 342 ₂ , 354 ₂ , 374 ₂ , 378	351, 367, 368 ₂ , 373
382	354 ₂ , 374, 379	367, 368, 373 ₂ , 381
383	378 ₂ , 384	367
384	381	378 ₂
385	381 ₂	378

TABLE 29

Family H.—Progeny of plant 44 (F_1 , cross No. 2, class C) \times plant 10 (F_1 , cross No. 2, class A) grouped in accordance with their behavior in inter-crosses.

Group	Ped. No.	No. cases fertile within group					No. cases sterile within group				
		A	B	C	D	Ind.	A	B	C	D	Ind.
A	315	0	—	—	—	—	5	—	—	—	—
	316	1	1	—	—	—	6	0	—	—	—
	317	0	2	—	—	1	8	0	—	—	0
	318	1	1	—	1	—	5	0	—	0	—
	319	0	0	—	—	1	4	1	—	—	0
	321	0	3	—	—	—	6	0	—	—	—
	322	0	2	—	—	1	4	0	—	—	0
	324	2	3	1	—	1	7	0	0	—	0
	327	0	3	—	2	1	10	0	—	0	0
	328	3	2	—	—	—	8	0	—	—	—
	329	0	1	—	—	2	5	0	—	—	0
	330	0	1	—	—	—	4	0	—	—	—
	331	0	1	—	—	1	8	0	—	—	0
	334	0	1	—	—	—	5	0	—	—	—
	336	1	1	—	1	1	5	1	—	0	0
	337	1	—	—	2	2	7	—	—	0	0
	340	0	1	—	1	2	7	0	—	0	0
	342	1	6	—	2	3	9	1	—	0	0
	345	0	—	—	—	—	5	—	—	—	—
	346	0	—	—	—	—	1	—	—	—	—
	349	0	2	—	—	1	2	0	—	—	0
	350	0	2	—	—	—	7	0	—	—	—
	353	0	1	—	—	—	2	0	—	—	—
	354	1	7	0	—	3	13	0	1	—	0
	358	0	—	—	—	—	2	—	—	—	—
	359	0	1	—	—	3	6	0	—	—	0
	360	0	—	—	—	1	2	—	—	—	0
	362	0	3	—	—	—	8	0	—	—	—
	363	0	2	—	—	1	5	0	—	—	0
	365	0	1	—	—	2	6	0	—	—	0
	370	0	3	1	—	—	3	0	0	—	—
	371	1	4	—	—	1	6	0	—	—	0
	372	0	3	—	—	—	3	0	—	—	—
	374	0	4	?	—	—	8	0	0	—	—
B	320	8	1	—	—	—	1	4	—	—	—
	335	8	0	—	—	—	1	2	—	—	—
	348	1	0	—	—	1	0	2	—	—	0
	351	9	0	—	—	2	0	4	—	—	0
	352	3	0	—	—	—	0	1	—	—	—
	367	5	1	0	—	—	0	4	1	—	—
	368	8	0	—	—	1	0	6	—	—	0
	373	5	1	2	—	—	0	4	1	—	—
	381	11	1	4	—	2	1	6	0	—	0
	382	2	0	1	—	—	0	4	0	—	—
C	383	—	0	3	—	—	—	1	0	—	—
	378	2	3	0	—	—	0	1	3	—	—
	379*	2	3	0	—	—	1	1	1	—	—
	384	—	2	0	—	—	—	0	1	—	—
D	385	—	2	0	—	—	—	0	1	—	—
	338	3	—	—	0	1	0	—	—	1	0
Ind.	339	6	—	—	0	—	0	—	—	1	—
	325	4	—	—	—	—	0	—	—	—	—
	333	1	—	—	—	—	0	—	—	—	—
	341	5	—	—	—	—	0	—	—	—	—
	347	8	1	—	—	—	0	0	—	—	—
	355	4	2	—	—	—	0	0	—	—	—
	366	6	2	—	—	—	0	0	—	—	—

* Probably not really a member of group C.

sterile reciprocal, plus the 56 self-combinations. The probable total sterility in the population is 54.0 percent \pm 1.4 percent, therefore, which makes it unlikely that more than 3 or 4 intra-sterile classes are present. These matings are shown in table 28.

The individuals are grouped with reference to their behavior in intercrosses in table 29. This table appears to reveal 4 classes containing 34, 11, 4 and 2 plants, respectively, in addition to 6 indeterminate individuals. Let us see what it really shows.

In the first place, there are 8 exceptions—fertility where there should be sterility—in the fertility columns. They are as follows, each mating being made but *once*.

Class A	316 \times 324
“ “	318 \times 328
“ “	324 \times 342
“ “	328 \times 337
“ “	336 \times 328
“ “	354 \times 371
Class B	320 \times 381
“ “	373 \times 367

There are also 6 exceptions—sterility where there should be fertility—in the sterile columns, and here one mating (No. 4) was made twice and one mating (No. 6) three times. These exceptions are as follows:

1. B \times A 319 \times 381
2. B \times A 320 \times 342
3. B \times A 335 \times 336
4. C \times A 379 \times 354
5. B \times C 367 \times 378
6. C \times B 379 \times 373

These exceptions are no more than were to have been expected from the predictions made above from *a priori* calculations. Of the fertile exceptions, at least 5 were made at the last of the season. No data regarding percentage of seed obtained to seed expected in full capsules were recorded, unfortunately, but it is probable from our other experiences that the majority of them produced only partly filled capsules, and would have proved sterile had they been made earlier. The sterile exceptions 379 \times 354 and 379 \times 373, made twice and thrice respectively are of little consequence because 379 falls into class C only through the single sterile mating 378 \times 379 (made twice). Thus we could just as

reasonably call 379 an indeterminate,—that is a plant fertile in all combinations tried,—and have but the sterile exception 378×379 for which to account. It could not go into groups A or B, though sterile with one plant of each of those groups because it also was fertile with 2 members of group A and with 3 members of group B.

This interpretation may be made either way without affecting the chief point the table was designed to show. No indeterminate individual and neither plant of the very uncertain class D, which was based on the single case of sterility 339×338 , were crossed with plants of class C. Therefore the 3 classes A, B and C are the only ones for which we can claim independence.

A meaning can now be given to the results of the back-crosses which were listed in table 27. 38 plants were crossed with pollen from one or both parents. Out of the 23 plants crossed with No. 44 just 1 was sterile,—a single pollination of 366×44 . It is possible that this mating also might have shown fertility if tested further, but it may show that 366 is the only plant among those tested that belongs to the same intra-sterile class as 44.

Plant 10 was used as pollen parent with 29 plants, of which 10 produced some seed. Plant 342 produced a few seeds which seemed to be parthenocarpic out of 4 tests, and plant 362 yielded 8 seeds in 1 of the 4 tests made. Therefore we have no hesitancy in classifying them as sterile. Plant 314, which was fertile to plant 10 pollen, was discarded early and is not classified in table 29. For this reason it may be left out of consideration. Plants 335 and 367 were fertile in one pollination each, and sterile in one pollination each. Since they gave full capsules in each of the successful pollinations, however, let us record them as fertile. Now what is the result? *Out of 20 sterile matings 18 are with plants belonging to class A.* The first exception is with the plant 379 which behaved so irregularly—as shown by table 29—that it is just as likely to be a member of class A as class C. The second exception is a single pollination with plant 385 of class C. *Fertility is shown in 7 cases, all of which are with class B.* Furthermore, the 3 sterile matings made with pollen from plant 34, a member of the same F_1 class as plant 10, are with plants of class A of family H. And the 1 sterile mating made with plant 18, a plant of F_1 class B, is with plant 339, a member of class D of family H. Therefore, it seems unquestionable that Plant 44 (and thus class A of F_1) belongs to the class A of family H.

TABLE 30
Family I.—Record of cross-pollinations on progeny of plant 44 (F., cross No. 3, class C) × plant 34 (F., cross No. 2, class A) outside family I.

Ped. No. ♀	Fertile with parents ♂	Sterile with parents ♂	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
387	44			
391	44	34 _a		372 _a fam. H
392				
394	44 _a			
395	44			315 fam. H, 317 fam. H
396	44			
398	44, 34 _a			
400	44	34 _a		
401	44	34 _a		
405	44 _a		351 fam. H	10 _a F., 354 fam. H, 374 fam. H
408	44		337 fam. H, 477 fam. J, 524 fam. K	354 fam. H, 374 fam. H
409	44			
412	44, 34 _a late	34 _a		
413	44	34 _a	374 fam. H	
415	44	34 _a	490 fam. J	354 fam. H, 374 fam. H
421				
425	34			
426	44 _a	34 _a		
430	44	34 _a		
431	44, 34 _a			377 fam. H
432			377 _a fam. H	
433	44		381 fam. H	
440	44 _a			
442	44			
444	44 _a			
446	44	34		
448			474 fam. J, 475 fam. J	
451	44 _a	34 _a		
455	44 _a	34 _a		
456	44 _a	34 _a		
457	44 _a			
458		34 _a	320 fam. H, 381 fam. H	380 fam. H
460				
463	44			
465	44		278 _a fam. G, 320 fam. H, 381 fam. H, 489 fam. J	374 _a fam. H
467	44			
468		34 _a		
470		34 _a		

TABLE 31

Family I.—Record of cross-pollinations on progeny of plant 44 (F_1 , cross No. 3, class C) \times plant 34 (F_1 , cross No. 2, class A).

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
387	395, 396	
390		396 ₂
391		396 ₂
392		395, 444, 468 ₂
394	390, 396, 398, 400, 405	
395		400, 405 ₂
396	413	400, 401, 405, 415
398	396, 400	413
400	401	396 ₂
401		405, 415, 426, 467
405	398, 413	401, 408, 415, 467 ₂
408	413	405, 409, 415, 426
409		408 ₂
412	420	
413	396, 401, 405, 408, 415, 418, 420	
414	425 ₂	415 ₂
415	413, 425	401, 405, 412, 414, 420, 426, 458
418	431	412 ₂
420	431, 425	401, 405, 415, 425, 426, 458
421		467
425		431
426	425, 433	405, 420, 440, 445, 458, 464 ₂
430	426, 433	431, 458
431	401, 426, 433, 439, 455	430, 440
432	431 ₂	
433	405, 426, 431, 439, 440, 451, 458	
439	433	440, 444
440	433	415, 426, 439, 444, 451, 457
442	439, 446	444, 451
444	431, 456, 458 ₂	440, 451
445		
446	442	430, 431
448		421 ₂
451		442, 444, 455, 467
455		415, 426, 440, 451, 456 ₂
456	444	455, 457, 458, 467 ₂
457	463	455, 456, 458, 467
458	413	405, 420, 451, 455, 456, 467
460		392, 468 ₂
463	456, 457, 465	
464		
465	456, 463	457 ₂
467		455, 456 ₂
468		
470		465 ₂

Family I.—Plant 44 of class C, cross No. 3 \times plant 34 of class A, cross No. 2

Family I was produced from seed obtained by pollinating plant 44 of class C, cross No. 3, with pollen of plant 34 of class A, cross No. 2. It is therefore a test of the similarity of constitution of plants of class A

of F_1 , since plant 44 was crossed first with plant 10 of class A to produce family H and then with plant 34 of class A to produce family I.

83 greenhouse plants were grown; but the task of manipulating that number proved too great and very nearly one-half of them were discarded after several weeks of work, permitting our efforts to be more concentrated. We have not thought it necessary to report any of the pollinations made on the rejects.

Of the plants remaining, 25 were selfed from 1 to 6 times between the first and the middle of the reproductive period without obtaining a single seed. Somewhat contrary to what might have been expected, 6 of these same plants were again selfed several times during the latter part of the season with the same result. This does not prove that no seed could have been obtained at that time if further pollinations had been made, however, as a few seeds were produced in a part of the pollinations of 22 cross-matings made during the waning of the flowering period, where continued pollinations made before had left no doubt as to the sterility of the combination. In 9 other matings, 1 pollination each produced no capsule, but in each case other matings—usually several—giving full capsules, proved them to be fertile. They were therefore so recorded.

Table 30 shows the record of back-crosses with pollen of the parents, and also the crosses made with plants outside of the family. It will be discussed after making the usual classification.

The inter-crosses in this family are shown in table 31. About one-sixth of the 2025 different combinations possible with 45 plants were accomplished. The table shows 61 fertile and 97 sterile matings, including 13 pairs of fertile reciprocals and 20 pairs of sterile reciprocals. The total number of different cross-combinations, therefore, is 250, made up of 96 fertile and 154 sterile combinations. Adding the 45 self-combinations, we have 199 steriles out of a total of 295 combinations. The probable sterility in the population is thus 67.5 percent \pm 1.8 percent, and we should scarcely expect more than 3 or at most 4 intra-sterile classes even if a Mendelian dominant type ($3 + 1$) of distribution in the classes be assumed.

The grouping actually obtained is set forth in table 32. Three classes containing 34, 4 and 2 individuals, respectively, and 5 unplaced plants, appear. There are 6 fertile exceptions:

400 \times 401

412 \times 420

442 \times 439

444 \times 456

444 \times 458

465 \times 456

TABLE 32

Family I.—Progeny of plant 44 (F_1 , cross No. 3, class C) \times plant 34 (F_1 , cross No. 2, class A) grouped in accordance with their behavior in inter-crosses.

Group	Ped. No.	No. cases fertile within group				No. cases sterile within group			
		A	B	C	Ind.	A	B	C	Ind.
A	390	0	—	—	1	1	—	—	0
	391	0	—	—	—	1	—	—	—
	392	0	—	—	—	4	—	—	—
	395	0	—	—	1	3	—	—	0
	396	0	—	2	2	6	—	0	0
	400	1	—	1	1	2	—	0	0
	401	1	1	1	—	6	0	0	—
	405	0	—	2	2	10	—	0	0
	408	0	—	1	—	4	—	0	—
	409	0	—	—	—	1	—	—	—
	412	1	—	—	—	2	—	—	—
	414	0	1	—	—	1	0	—	—
	415	0	1	1	—	10	0	0	—
	418	0	1	1	—	1	0	0	—
	420	1	1	—	—	5	0	—	—
	421	0	—	—	—	2	—	—	—
	426	0	3	—	1	10	0	—	0
	439	1	1	—	1	2	0	—	0
	440	0	0	—	1	7	1	—	0
	442	1	1	—	—	2	0	—	—
	444	2	2	—	—	5	0	—	—
	445	0	—	—	—	1	—	—	—
	448	0	—	—	—	1	—	—	—
	451	0	—	—	1	6	—	—	0
	455	0	1	—	—	7	0	—	—
	456	2	—	—	1	4	—	—	0
	457	0	—	—	1	6	—	—	0
	458	1	0	1	1	9	1	0	0
	460	0	—	—	—	2	—	—	—
	464	0	—	—	—	1	—	—	—
	465	1	—	—	1	2	—	—	0
	467	0	—	—	—	8	—	—	—
	468	0	—	—	—	2	—	—	—
	470	0	—	—	—	1	—	—	—
B	425	4	0	—	—	0	1	—	—
	430	1	0	—	1	1	2	—	0
	431	6	0	—	2	1	3	—	0
	446	2	0	—	—	0	2	—	—
C	398	3	—	0	1	0	—	1	0
	413	8	—	0	—	0	—	1	—
Ind.	387	2	—	—	—	0	—	—	—
	394	4	—	1	—	0	—	0	—
	432	—	1	—	—	—	0	—	—
	433	6	2	—	—	0	0	—	—
	463	3	—	—	—	0	—	—	—

TABLE 33
The behavior of individuals of the various groups of family I toward individuals of the various groups of family H.

Class of fam. I	Ped. No. of fam. I	Fertility with individuals of family H				Sterility with individuals of family H			
		Class A	Class B	Class C	Ind.	Class A	Class B	Class C	Ind.
A	392								
	396								
	401								
	405		351, 381			372 315, 317 354 recip., 374 recip. 354, 374			
	408								
	415	337	381			354, 374			
	440		381						
B	458		320, 381						
	460								
	467	337, 371	320, 368, 381			342 374 reciprocal			380
C	431								
Ind.	413	374							377
	432				377				

Four of these matings were made but once, 1 was made twice and 1 was made reciprocally. The last 2 and 1 other were end-season matings, the others were mid-season matings. There are 2 sterile exceptions, 431×440 and 430×458 , each tried but once. The number of combinations that form the basis of our grouping is so large, that there is little danger in accepting the classification as given, however, since these errors might have crept in in various other ways, as has been shown before. But it should be mentioned that plant 430 falls just as readily into group A as it does into group B.

The evidence in this table does not support the idea of more than 3 classes. A and B are well established. But C may be B, since neither members of the class were crossed with any B individuals. Of the indeterminates, 387, 394 and 463 may be B and 432 may be A. The sole positive evidence of a third class, therefore, rests upon plant 433, which is not A (6 matings in evidence) nor B (2 matings in evidence).

Let us now consider the back-crosses shown in table 30. Every cross made with the pollen of plant 44, 29 in number, was fertile. On the other hand 15 back-crosses with pollen from plant 34 were sterile, though an average of over 3 pollinations per plant was made. Seed was obtained in only 1 instance: 4 pollinations were made on plant 412, and 2 made late in the season gave some seeds. The interesting feature in these 15 sterile matings is that 14 of them were made on plants of class A, and the fifteenth on plant 430, which, though tabled in class B may just as readily be placed in class A.

But 3 plants were fertile to pollen of plant 34,—plants 425 and 431 of class B and plant 398 of class C.

A single mating of plant 10 on plant 401 of class A was sterile. Since plant 10 and plant 34 belong to the same class of the F_1 generation, this mating may be compared with the 3 sterile matings of class A plants of family H with pollen from plant 34.

Note then the similarity between families H and I. Each has 3 independent inter-fertile, intra-sterile groups with almost the same distribution of individuals within the classes; each behaves similarly in back-crosses. With the exception of a single unclassified plant of family H, all of the plants tested of both families were fertile with plant 44 of class C of the F_1 generation, the female parent of both. With regard to plants 10 and 34, the male parents of families H and I respectively, both of which belonged to class A of the F_1 generation, each was sterile with class A plants of both families and each fertile with other plants of their respective families. The conclusion is unavoidable, therefore, that class

A of the F_1 generation, class A of family H, and class A of family I, are identical.

This is not the only evidence that can be brought forward in favor of the similarity of these two families. A sufficient number of crosses (table 33) was made between the two populations to prove that class A of family H and class A of family I are the same. Ten members of class A of family I were crossed with plants from family H. Three pairs of reciprocals were made with like results for each pair. Counting these pairs as but 1 mating each, members of class A of family I were crossed 14 different ways with members of class A of family H. Of these matings 11 were sterile, and 3 fertile. But of the fertile matings, 2 were with 337 and did not give full capsules. These same class A plants of family I were also mated 9 times with members of class B of family H, and all matings were fertile. Bearing these results in mind, the single sterile mating of 460,—family I, class A,—with 380,—unplaced member of family H,—is pretty good evidence for placing 380 in class A of family H. Likewise, the sterility between 431 and 377 is evidence that 377 of family H is not a member of that family's class A, a conclusion supported by its fertility with unplaced 432 of family I. The remaining cross, plant 413 of class C of family I with plant 374 of class A of family H, was fertile.

We do not believe it rash to assert that this makes a complete case. There can be no doubt that families H and I are practically duplicates of each other. *In this instance, then, two plants belonging to a single class in which all of the individuals were cross-sterile with each other, when crossed with the same individual have produced populations as similar to each other in their behavior in crossing as if they were samples of the same population.*

This does not prove that all members of an intra-sterile class crossed with the same individual would produce identical populations. No such claim is made. It does indicate very strongly, however, that in this particular case, these 2 plants of the F_1 class A (10 and 34) are identical in that part of their constitution which affects self- and cross-sterility. The criticism may be offered that these results show merely a kind of dominance exhibited by plant 44, but if this be true, it is a dominance of a strikingly perfect kind.

Family J.—Plant 52 of class B, cross No. 3 \times plant 23 of class A, cross No. 2

As has just been shown, F_1 plants of class C when crossed with their

TABLE 34

Family J.—Record of cross-pollinations on progeny of plant 52 (F_1 , cross No. 3, class B) \times plant 23 (F_1 , cross No. 2, class A) outside family J.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
475	524 fam. K	
477	377 fam. H, 467 fam. I	
487	512 fam. K	
489	467, fam. I	
490	421 fam. I	
495	18 F_1	
499	18, F_1	
502	18 F_1 , 512 fam. K	

sisters of class A give populations having a high percentage of cross-sterility and by the same token a small number—2 or 3—of intra-sterile groups. Family J tests the behavior of an F_1 plant of class B with a class A sister.

30 plants of this family were grown in the greenhouse, 6 dying or being discarded. They were all selfed from 1 to 12 times with no production of seed except on plants 473 and 489. These 2 individuals produced seed the latter part of the flowering season. No. 473 was selfed 7 times at various periods. The first 2 pollinations yielded no seed, the third and fourth a few seeds, and the last 3 half-filled capsules. No. 489 was selfed 9 times. The first 3 were failures; the remainder induced capsules, the last 3 pollinations producing a full quota of seed.

Only 1 back-cross was made. No. 474 was fertile with No. 52.

The few other crosses made with plants outside the family are recorded in table 34. All were successful. It should be noted that 3 of these successes were with plant 18, another member of class B of the F_1 generation.

As usual only a comparatively few of the 576 combinations possible between 24 plants were made. The record of cross-pollinations listed in table 35 are sufficient, however, to show the striking difference in percentage of cross-sterility between this family and the 2 families just described. There are 65 fertile matings including 14 pairs of fertile reciprocals, making 102 fertile combinations in all. Since there are no sterile reciprocals, the 13 sterile matings are equivalent to 26 sterile combinations. Adding the 24 self-combinations, gives a ratio of sterility to total combinations of 50 : 152. The probable sterility in this family

is therefore 32.9 percent \pm 2.6 percent, which leads us to expect about 5 intra-sterile groups.

The grouping made possible by the sterile matings is shown in table 36. There are no exceptions. Each individual in every group shows perfect inter-class fertility and intra-class sterility as far as they were

TABLE 35

Family J.—Record of cross-pollinations on progeny of plant 52 (F_1 , cross No. 3, class B) \times plant 23 (F_1 , cross No. 2, class A).

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
473	474, 475 _a , 485 ₂	480
474	475 _a , 480 ₂ , 482, 485	
475	474, 477, 480, 482, 485 ₄	
477	473, 475 _a , 482, 485 _a	
478	484, 485	
480	474, 475 _a , 482, 486, 487 ₂ , 491	
482	474, 484, 485 ₂	
484	474, 480, 482, 487 ₂	485 ₂
485	474, 475, 482 _a , 492	484
486	485, 492 _a	474, 495
487	474, 482, 484, 486, 492, 499	
488	482, 487,	484
489	477, 492	486
490	489	
491	480	484
492	484, 487 ₂ , 493, 495 ₂	
493		502
494		486, 502
495	499	
496		492
499	502 ₂ , 503	
500	486, 493, 499, 502, 503	
502	499	495
503	499 _a , 500, 502 ₂	

tested. Apparently there are 4 classes containing 7, 4, 2 and 2 individuals, respectively, together with 9 plants which showed no cross-sterility and are unplaced.

Table 37 shows the evidence for independence between these groups more clearly. A, B and C or D must be independent, but C and D may belong to one class since they were not crossed together. In addition 475, 477 and 482 are independent of each other and of A, B and C. Thus there are apparently 6 independent classes with frequencies of 7, 4, 2, 1, 1 and 1, these frequencies being subject to change of course given the data necessary to fit the remaining individuals into their proper niches. Before accepting this classification at its face value, however, we ought

TABLE 36

Family J.—Progeny of plant 52 (F_1 , cross No. 3, class B) \times plant 23 (F_1 , cross No. 2, class A) grouped in accordance with their behavior in inter-crosses.

Group	Ped. No.	No. cases fertile within group					No. cases sterile within group				
		A	B	C	D	Ind.	A	B	C	D	Ind.
A	474	0	2	2	—	3	1	0	0	—	0
	486	0	1	1	1	2	4	0	0	0	0
	489	0	—	—	1	2	1	—	—	0	0
	493	0	—	—	1	1	1	—	—	0	0
	494	0	—	—	—	—	2	—	—	—	—
	495	0	—	—	1	1	2	—	—	0	0
	502	0	—	—	—	3	3	—	—	—	0
B	484	1	0	1	1	3	0	3	0	0	0
	485	1	0	1	1	4	0	1	0	0	0
	488	—	0	—	—	2	—	1	—	—	0
	491	—	0	1	—	—	—	1	0	—	—
C	473	1	1	0	—	2	0	0	1	—	0
	480	2	2	0	—	3	0	0	1	—	0
D	492	4	2	—	0	1	0	0	—	1	0
	496	—	—	—	0	—	—	—	—	1	—
Ind.	475	1	1	2	—	2	0	0	0	—	0
	477	1	1	1	—	2	0	0	0	—	0
	478	—	2	—	—	—	—	0	—	—	—
	482	1	3	1	—	3	0	0	0	—	0
	487	2	2	1	1	2	0	0	0	0	0
	490	1	—	—	—	—	0	—	—	—	—
	499	2	—	—	—	3	0	—	—	—	0
	500	3	—	—	—	2	0	—	—	—	0
	503	1	—	—	—	2	0	—	—	—	0

TABLE 37

Family J.—Progeny of plant 52 (F_1 , cross No. 3, class B) \times plant 23 (F_1 , cross No. 2, class A) grouped to show inter-class fertility.

	A	B	C	D	475	477	478	482	487	490	499	500	503
A		3	3	4	1	1		1	2	1	2	3	1
B	2		3	2	1	1	2	3	2				
C	3	3		2	1		1	1					
D	4	2							1				
475	1	1	2			1		1					
477	1	1	1		1			1					
478		2											
482	1	3	1		1	1			1				
487	2	2	1	1					1		1		
490	1												
499	2								1			1	1
500	3										1		1
503	1										1	1	

to see whether the independence of any of the 3 single plants is based upon a single pollination. Plants 475 and 477 were fertile reciprocally, 4 pollinations being made in all, but plants 475 and 482, and plants 477 and 482 were crossed but once. This is also true of the basis of independence between 477 and A, 477 and C, and 482 and C. It depends on 1 pollination in each case.

For these reasons it is hardly likely that more than 6 independent classes exist in this population, and the chances are perhaps even that there are only 5. Nevertheless, family J unquestionably contains 2 or 3 more intra-sterile classes than family H or family I.

TABLE 38

Family K.—Record of cross-pollinations on progeny of plant 52 (F_1 , cross No. 3, class B) \times plant 44 (F_1 , cross No. 3, class C).

Ped. No. ♀	Fertile with parents ♂	Fertile with Ped. No. outside family ♂	Fertile with Ped. No. within family ♂	Sterile with parents ♂	Sterile with Ped. No. outside family ♂	Sterile with Ped. No. within family ♂
505						508
507			515			
508						505
509						
511	44, 52 ₁		508, 509			512 ₂
512	52			44		520
515			524	44		
517				44		
520	52			44 ₁		524
521	44, 52		512			512 ₂
524	44, 52	58 <i>N. alata</i>				
525			520 ₂			
527			505 ₂ , 509			
528	52 ₁		58 ₂ <i>N. alata</i>			

Family K.—Plant 52 of class B, cross No. 3 \times plant 44 of class C, cross No. 3

Very little was done upon family K, as table 38 shows, though this family resulting from crossing a plant of class B (52) with our much used plant 44 of class C, might have proved very interesting. The plants would possibly all have shown fertility in back-crosses with 52, while only a part would have proved fertile with the other parent. This is the indication of the few matings made. There were 6 cases of fertility and none of sterility with No. 52, and 3 cases of fertility and 4 of sterility with 44.

2 plants were crossed with *N. alata* plant No. 58; both were successful. These were the only crosses made outside of the family with K plants

used as females. But K pollen was fertile on several plants of other families; viz., 524 on 337 of family H, on 408 of family I, and on 475 of family J; 512 on 487 and 502 of family J.

The 14 matings made within the family, including as they do 2 pairs of sterile reciprocals, are hardly a sufficient basis for even a guess as to the amount of cross-sterility present potentially. We can only say that the number of intra-sterile classes would not have been large, the percentage of sterility probably lying between 35 and 50.

Argument on cross No. 2 and cross No. 3

If further evidence of the beautiful regularity with which plants belonging to the same intra-sterile class behave in crosses be desired, it is found in the crosses between families cited in tables 13, 18, 22, 27, 30, 33 and 34.

Plants 152 and 153 of class A, family D, were both sterile with family E pollen which is presumably of one kind. The mating 152 D \times 204 E was even made reciprocally. Plants 167 and 171 of family D, which were discarded after a few matings had been made and were therefore undetermined as to class, were fertile to pollen of family E.

In family F, plants 216, 239 and 243, all of class B were each sterile with the pollen from the unplaced plant 247 of family G. Plant 244, an unplaced plant of family F was fertile with the pollen of 247, however. On the other hand, plants 216 and 241 of family F, class B were fertile with the pollen of plants 278 of class C, family G and 250 of class A, family G, respectively. Plant 278 of class C, family G, was also fertile with the pollen of plant 219 of class A, family F, although plant 219 was sterile with the pollen of plant 250 of class A, family G.

If we may say that sterility shows likeness of constitution and fertility unlikeness of constitution, these results show: (1) that class A of family F and class A of family G are alike; (2) that class A of family F and class C of family G are unlike; (3) that class B of family F and classes A and C of family G are unlike, as they should be since classes A of both families are alike; and (4) that the unplaced plant 247 of family G belongs in with class B of family F, as might very well be the case.

In the remaining matings between plants belonging to different families there was no sterility, except among those matings between families H and I already discussed. They are none the less interesting, however, because they show that once fertility has been found between classes belonging to different families, all matings between plants belonging to these classes will prove fertile barring experimental error.

In family G, unplaced plant 249 was fertile with plant 351 of class B, family H and with plant 467 of class A, family I. Plant 278 of class C was fertile with pollen from plant 374 of class A, family H. Plants 278 and 281, both members of class A, were also fertile with plants 467 and 405 of class A, family I, respectively. Thus 2 combinations between the classes A of families H and I proved to be fertile.

Likewise, 3 plants of class A, family H, 317, 319 and 321, proved to be fertile with the pollen of plant 311 of class F, family G. Another plant of class A, 337, also proved to be fertile with the unplaced plants 477 of family J and 524 of family K.

Fertile matings were made as follows between 4 plants of class A, family I, and plants of families G and J; 408 with 477, of family J unplaced; 421 with 490, of family J unplaced; 448 with 474 of family J, class A, and with 475 of family J unplaced; 467 with 278 of family G, class C, and with 489 family J, class A.

Fertile matings were also made with the pollen of 3 family I, class A plants on plants of family J. Pollen of 467 was fertile on 477 unplaced and on 489, class A of family J, and pollen of 421 was fertile on 490 unplaced of family J.

Thus plants of class A of family I were fertile once with a plant of class C, family G, 4 times including a reciprocal with unplaced plants of family J, and 3 times including a reciprocal with plants of class A, family J.

In these matings between families, then, not a single one militates against our conception of inter-fertile, intra-sterile groups. We believe, therefore, that the fundamental basis of this grouping is established beyond doubt, and that the actual groups as submitted in the foregoing pages are sufficiently exact to be made the foundation of a theoretical interpretation of the behavior of self-sterile plants among themselves.

Undoubtedly there will come the critic who will say we have been at some pains to make out a case for the presence of inter-fertile, intra-sterile classes in this family. He will point out that some of the exceptions among the matings may not have been due to experimental errors and hence must have subtle meanings other than those given, that our phrase "pseudo-fertility due to environment" veils the real facts. Let us forestall him.

Of course *some* of the matings which form exceptions to the rule of inter-fertile, intra-sterile classes may be the effect of an unknown biological cause; certainly factors other than environmental may be the

basis of a portion of the change from sterility to partial fertility in certain matings as the flowering season wanes.

The first thing to establish, however, was a broad general rule for the behavior of self-sterile populations. This has been done by the work on these 2 crosses. *The members of any population of the self-sterile species under consideration fall naturally into a relatively small number of groups, each individual being cross-sterile reciprocally with every member of the same group and cross-fertile reciprocally with every other individual.* The sum total of the exceptions to this rule is well within the limits of experimental error, even though the question is one in which every bit of evidence, like pieces of a jig-saw puzzle, must fit, if a solution is to be obtained. The exceptions to the rule, in fact are of another order of magnitude than the confirmations. If, therefore, true exceptions do occur, they are so rare that the usefulness of the rule is not in the least impaired. Other general matters must be settled before it is even desirable to endeavor to inquire into them.

Lest there be some difficulty in carrying in mind the essential facts regarding the grouping of the plants of this series, let us summarize them here.

The two self-sterile species *N. Forgetiana* and *N. alata* were crossed reciprocally. The progeny of these two crosses behaved so similarly that collectively the 53 individuals studied could be placed in 6 intra-sterile classes 5 of which were proved to be independent. The remaining questionable group consisted of one plant.

From this population 8 families were raised which were characterized as follows:

D = *N. alata* plant 53 \times plant 44, class C; probably consisted of 4-6 classes, 3 being established.

E = *N. alata* plant 58 \times plant 44, class C; probably consisted of 1 class.

F = plant 34, class A \times plant AA, *N. Forgetiana*; probably consisted of 5-6 classes, 4 being established.

G = plant 44, class C \times plant AA, *N. Forgetiana*; probably consisted of 4-6 classes, 3 being established.

H = plant 44, class C \times plant 10, class A; probably consisted of 3 classes, 3 being established.

I = plant 44, class C \times plant 34, class A; probably consisted of 3 classes, 3 being established.

J = plant 52, class B \times plant 23, class A; probably consisted of 5-6 classes, 5-6 being established.

K = plant 52, class B \times plant 44, class A; probably consisted of 4-6 classes.

It was also determined that class A of the F_1 generation, class A of family H, and class A of family I are identical.

Cross No. 4. N. commutata \times *N. Forgetiana* (self-sterile \times self-sterile)

The race used here with the pollen of *N. Forgetiana* was received from Italy under the name *N. commutata* Fisch. and Meyer. It is the plant called *N. Langsdorffii* Weinm. variety *grandiflora* by COMES (1899). Of it he says: "Elle est connue depuis 1835 dans les jardins européens, mais on en ignorait la patrie." It has been duplicated in our experiments by crosses between *N. alata* and *N. Langsdorffii*. It is an additional argument in favor of such an origin, that it is self-sterile, since *N. Langsdorffii* is always self-fertile. When crossed with *N. Langsdorffii* the F_1 plants are self-fertile. The behavior of this race when crossed with *N. Forgetiana* is interesting, therefore, whether it be a true wild species or was produced by hybridization. In the first case, a new species cross is reported, in the second case, a self-sterile race extracted from a cross between a truly self-fertile species and a self-sterile species, is crossed again with a different self-sterile species.

The F_1 plants were highly fertile, in the sense that 90-100 percent of the pollen was normal in nearly every plant, and that "proper" combinations yielded full capsules.

A rather small number, 12, field-grown F_1 plants were used in our experiments. These were selfed from 3-10 times, an average of over 4 pollinations per plant. 11 were completely self-sterile, yielding not a single seed. Plant No. 3, however, produced 4 good capsules out of 4 pollinations. This plant behaved like a real self-fertile. Crossed as a female with each of the other 11 individuals it was fertile; crossed as a male with all but plants 5 and 11, it was also fertile. Further, it was fertile as a female with *N. Forgetiana*. The meaning of this behavior has not been determined conclusively. Two interpretations are possible. Owing either to its hybrid origin (self-fertile \times self-sterile) or to a recent introduction of *N. Langsdorffii* "blood," the race is a mixture of self-fertile and self-sterile plants; or, by reason of its having been grown near *N. Langsdorffii* the preceding generation, the seed from which this plant came was produced by a stray pollen grain of that species. The second interpretation seems more probable, since we have corroborated

TABLE 39

Result of matings on F₁ plants of cross No. 4, N. commutata × N. Forgetiana.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
1	3 _s	2 _s , 4 _s
2	3 ₂	1 _s , 4 _s
3	1 _s , 2 _s , 4 _s , 5 _s , 6 _s , 7 _s , 8 _s , 9 _s , 10 _s , 11 _s , 12 _s	
4	3 ₂ , 5 ₂ , 6 _s	
5	8 _s , 10 _s	6 _s , 7 _s
6	1 _s , 3 _s , 4 _s , 8 _s , 10 _s , 12 _s	5 _s , 7 _s , 9 _s , 11 _s
7	3 _s , 4 _s , 12 _s	5 ₂ , 11 _s
8	1 _s , 2 _s , 3 _s , 4 _s	9 _s , 10 _s
9	1 _s , 2 _s , 3 _s , 4 _s , 12 _s	7 _s , 8 _s
10	1 _s , 2 _s , 3 _s , 4 _s , 12 _s	7 _s
11	1 _s , 2 _s , 8 _s , 10 _s	5 _s , 9 _s
12	3 _s , 7 _s , 11 _s	1 _s , 2 _s , 4 _s

TABLE 40

Plants of F₁ generation, cross No. 4, grouped in accordance with their behavior in inter-crosses.

Group	Ped. No.	No. cases fertile within group			No. cases sterile within group		
		A	B	C	A	B	C
A	1	0	3	2	3	0	0
	2	0	2	2	3	0	0
	4	0	4	2	3	0	0
	12	0	4	1	3	0	0
B	5	1	0	2	0	3	0
	6	3	0	2	0	4	0
	7	2	0	0	0	4	1
	9	4	0	0	0	3	1
C	11	3	0	2	0	4	0
	8	3	3	0	0	1	1
	10	4	3	0	0	1	1

COMPTON's conclusion that true self-fertility is completely dominant over self-sterility.¹⁶

In this family 70 cross-matings were made, of which 48 were fertile and 22 sterile. These matings were each made more than once, as is shown by the subscripts in table 39. There were 22 pairs of fertile reciprocals and 4 pairs of sterile reciprocals. By multiplying the sterile and the fertile matings each by 2 and subtracting in each case the proper

¹⁶ The relation between self-fertile and self-sterile plants is to be made the subject of a later paper.

TABLE 41

*Intercrosses between progeny of pseudo self-fertile N. alata plant used in cross No. 2.
Compare with table 1.*

Ped. No.	Plants with which fertile		Plants with which sterile	
	as ♂	as ♀	as ♂	as ♀
53	57	58	54 _a	54 _a , 56, 59 _a
54			53 _a , 57 _a , 58 _a	53 _a , 59
56			53, 57, 58, 59	59 _a
57		53	58	54 _a , 56, 59 _a
58	53, 59			54 _a , 56, 57, 62, 64, 66, 71, 79
59		58	53 _a , 54, 56 _a , 57 _a	56
62			58, 79	66
64			58	
65			79	
66			58, 62, 71, 79	76, 78, 79
71			58	66
76			66	
78			66	
79			58, 66	62, 65, 66

number to allow for the reciprocals, we find that there were 52 fertile combinations and 36 sterile combinations.

If the self-fertile plant is omitted, there are 66 cross-combinations, each well established by more than 1 pollination through which one may group the remaining 11 individuals in intra-sterile classes. This grouping is shown in table 40. The 11 plants fall into 3 classes consisting of 5, 4 and 2 individuals. There is not a single case of intra-class fertility and but 2 instances of inter-class sterility. Matings 10 × 7 and 9 × 8 show sterility where fertility is to be expected.

Argument on cross No. 4

Outside of the fact that a plant which seems to be a true self-fertile appeared in this family and was tested with 11 self-sterile plants, no new phenomena are found in cross No. 4. The same cross-sterility, the same small number of inter-fertile, intra-sterile classes is found here that is found in crosses No. 2 and No. 3. Cross No. 4 merely furnishes corroboratory evidence of facts discussed earlier in the paper. It does show, however, that the facts discovered in crosses 1, 2 and 3, are not peculiar to a single hybrid.

INTRA-SPECIFIC PEDIGREE CULTURE EXPERIMENTS

Our experiments within each of these species can be described very briefly for they have been confined largely to self-sterility tests. Not a

single thorough inquiry into the cross-mating proclivities of the plants of a pure (?) species has been made. This may seem very odd when so much time has been spent on inter-specific crosses. But our resolution to favor the wider crosses is not without reason. We have satisfied ourselves that the crosses within a species behave in a manner similar to that of the crosses already described. It seems probable, therefore, that intra-specific crosses would provide no data that could not be obtained from inter-specific crosses, although the converse might not be true.

N. Forgetiana. Between 200 and 300 plants of *N. Forgetiana* have been selfed under various environmental conditions, with pseudo-fertility in only 3 instances, as has already been described. *N. Forgetiana* is therefore a species on which environmental variations have little effect. It is a species in which, if one could measure accurately the intensity of the particular environmental factors that affect the full production of self-sterility, either the norm for a standard average environment would stand markedly toward the *sterile* end of the scale, or the dispersion coefficient would be small. The environmental complex that tends towards the *greatest* amount of pseudo self-fertility is necessary for any visible effect on the plants.

A small number of intra-sterile classes has been shown to exist in *N. Forgetiana*. Judging from cross-sterility percentages, the probable maximum is between 5 and 8 groups, but no accurate classification has been made.

N. angustifolia. Between 80 and 100 plants of *N. angustifolia* have been tested for self-sterility without the production of a single seed. This work was done during three summer seasons on field-grown plants. A certain environmental variation obtained of course, but since no pollinations were made at the extreme end of a flowering season, one cannot maintain that no pseudo-fertility exists. We are only justified in stating that *N. angustifolia* is similar to *N. Forgetiana* in being difficult to influence by environmental changes.

Intra-sterile groups have also been demonstrated in this species. Their number has not been determined but is probably no greater than in *N. Forgetiana*.

N. alata. We have shown earlier that *N. alata* is a self-sterile species in which a considerable amount of pseudo self-fertility appears at the end of the flowering season under adverse conditions. In other words if the environmental factors affecting self-sterility could be measured as suggested in the case of *N. Forgetiana*, either the norm for a standard average environment would be further toward the *fertile* end of the

scale than in the latter species, or the dispersion coefficient would be larger.

As in the other two species, intra-sterile classes have been proved to exist, the maximum number probably being smaller than in *N. Forge-tiana* or *N. angustifolia*.

The most important new fact discovered in *N. alata* is the probability that a population may exist consisting of only one intra-sterile class (compare family E). Recall that self-sterility is a sporophytic character, that inbreeding decreases the number of intra-sterile classes, and that there is no physiological or morphological obstacle to the fusion of any two complemental gametes provided they meet. All of these facts favor the idea that the behavior of self-sterile plants among themselves,—given the presence of the character self-sterility through the presence of a homozygous factor X ,—is due to underlying causes which may be pictured as follows. A certain number of factors which affect self-sterility exist. The action of these factors is not cumulative. Mating is possible normally only to plants which differ in at least one of these factors.

If these premises be correct, after a very few generations of self-sterile plants raised from selfed seed by taking advantage of the phenomenon of pseudo self-fertility, one should find a population resulting from a single capsule which is homozygous for these effective factors and which is therefore wholly cross-sterile under normal conditions.

These conditions are very nearly met by the behavior of the grand-progeny of the original pseudo self-fertile *N. alata* plant that is recorded in table 1. Table 41 is made up from table 1 by tabling the cross-matings both ways when only made one way because of our belief that reciprocal crosses are always identical. By this table it appears that the 3 matings 53×57 , 58×53 , and 58×59 are fertile. Tabled both ways there are 6 fertile combinations. But let it be recalled that these matings were made during a long flowering season, and that during its wane several of the self-pollinations produced seed. What is more likely than that some sterile cross-matings should show pseudo-fertility at the same time? Our evidence is this. Of these matings 1 was made the middle of the season and did not give a full capsule, the other two were made at the end of the season. But this is not all. Our demonstration that every member of an intra-sterile class should be sterile with every other member is the result of an experience with nearly 10,000 cross-pollinations. The exceptions which have been met are very infrequent and are well within the expected experimental error. Now if table 41 be examined

carefully, it is seen that there is every indication that all of the 14 plants listed belong to *one class* and that the 3 apparently fertile matings are due to pseudo cross-fertility.

N. glutinosa. Not over a dozen plants of *N. glutinosa* have been tested for self-sterility. It appears to behave like *N. alata*. Cross-fertility has been demonstrated, but the number of cross-matings made is not sufficient to prove the existence of intra-sterile groups. The above statement also holds for the race described as *N. commutata*.

SUMMARY AND INTERPRETATION OF THE RESULTS

The experiments on the self-sterile species *Nicotiana Forgetiana*, *N. alata*, *N. glutinosa* and *N. angustifolia* described in the foregoing pages, concern only the behavior of self-sterile plants when bred *inter se*. All questions connected with the relation between true self-fertility and self-sterility have been omitted designedly as pertaining to a distinct problem. The inquiry thus limited is believed to have established the following points:

1. Self-sterility is inherited.
2. The four species *N. Forgetiana*, *N. alata*, *N. glutinosa* and *N. angustifolia* breed true to the tendency toward self-sterility.
3. Self-sterility is fully expressed in these species from the beginning to the middle of the flowering season. Toward the close of the flowering season, especially in plants exhibiting the effect of adverse environmental conditions, some self-fertility may be shown. That this phenomenon is simply a non-inherited fluctuation is confirmed in four ways: (a) the graduated character of the increased fertility as the flowering season wanes, (b) the return to complete self-sterility at the beginning of a second flowering season, (c) the sterility of all progeny raised from selfed seed, and (d) the failure to obtain an increased tendency toward self fertility after three successive generations had been raised from selfed seed of the most extreme variants. It has been called pseudo self-fertility.

This fact naturally shows that self-sterility, whatever its nature, is only a physiological impediment to self-fertilization.

4. Other environmental factors appear to have little or no influence on self-fertility.

5. The waning of the reproductive period affects *N. alata* and *N. glutinosa* more markedly than it does *N. Forgetiana* or *N. angustifolia*. This indicates multiple allelomorphism in a fundamental factor the presence of which is necessary for the development of self-sterility.

(N.B. This factor should not be confused with any of those assumed in the interpretation of the behavior of self-sterile plants among themselves).

6. Cross-sterility in its nature identical with self-sterility was found in every population of self-sterile plants tested. The percentage of cross-sterility in different populations, based in each case on numerous cross-matings, varied from 2.4 percent to 100 percent.

7. Omitting fluctuations toward self-fertility correlated with a waning flowering period and a few cases of true sterility as indicated by microscopical examinations of the pollen, no variability in fruitfulness was noticed in "fertile" combinations. Fertile matings always resulted in full capsules.

8. Self-sterility behaves as a sporophytic character. This is demonstrated by the behavior of reciprocal matings,—pairs of reciprocals always giving like results either when fertile or sterile. It follows from this fact that no selective fertilization occurs.

9. The F_2 generation of a cross between *N. Forgetiana* and *N. alata* showed a low percentage of cross-sterility, 2.4 percent. This cross was followed to the F_5 generation by means of successive sib matings. The F_5 generation showed 21.6 percent cross-sterility.

In a repetition of this cross made with different plants, several F_2 populations studied each showed much higher percentages of cross-sterility.

10. All of the individuals of a family arising from one mating may be fertile with both parents, but a part of the individuals may be sterile with one or with both parents.

11. Cross-sterility exhibits a regularity of behavior such that if A is sterile with B and with C, it may be predicted that B will be sterile with C. On the basis of this cross-sterility the plants in each family may be divided into a relatively small number of groups in which each member of a class is sterile with every other member of that class and fertile with every member of every other class.

12. The distribution of the individuals within each class in several of the families studied was such that the classes may not be assumed to be of the same size. In certain cases this distribution rather resembled that of the coefficients of a point binomial.

13. Assuming a point binomial distribution of individuals within the classes as a limiting type, the number of intra-sterile classes necessary to account for the highest percentage of cross-fertility found is estimated to be less than 25. In most of the families tested the number of intra-

sterile classes varied from 1 to 6. • In a cross between *N. alata* and *N. Forgetiana* in which 53 F_1 plants were tested rather thoroughly, 5 (or 6) such classes were found.

14. In those instances where a part of the individuals of a family were sterile to one or to both parents, only the members of a single class behaved in that manner.

15. Individuals belonging to different families as well as to different generations may belong to a single intra-sterile class.

16. Individuals belonging to different intra-sterile classes of the F_1 generation when mated with the same individual, produced populations varying in the number of intra-sterile classes.

17. Individuals belonging to a single intra-sterile F_1 class when mated with the same individual, sometimes produced populations having the same number of intra-sterile classes, a similar distribution of individuals within the classes, and possibly the same classes (see families H and I). It is not established that this behavior is universal, however. In the one case where the status of both the parents and the progeny as regards cross-sterility was established very definitely (families H and I), the two populations behaved in this manner; but in a case where the status of neither the parents nor their progenies (families D and E) was quite so clear, the two populations appeared to behave differently.

This rather varied series of facts can be given a very simple interpretation in keeping with recent interpretations of other inheritance phenomena provided judgment be suspended on one or two obscure points.

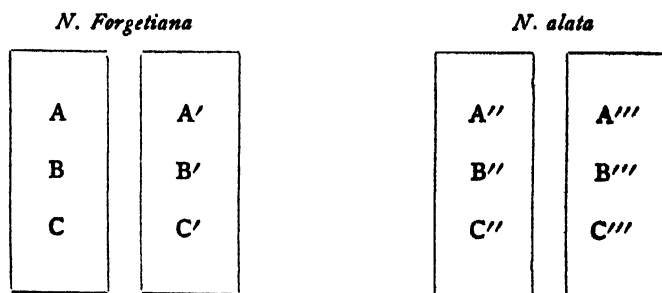
Let us assume first that a self-sterile species is self-sterile because it is homozygous for a fundamental self-sterility factor. Second, let us assume that a series of partially coupled factors affect the behavior of self-sterile plants among themselves. The action of these factors is on the sporophyte, and the nature of this action is such that two plants are not fertile together unless they differ by at least one of these factors.

It is not necessary to define the action of these factors more specifically, although this will be attempted in a subsequent publication. It may make matters somewhat clearer, however, to state that the immediate difference between a fertile and a sterile combination is in the rate of pollen-tube growth. If at the height of the season a series of self-pollinations and a series of cross-pollinations are made on a single plant and the pistils fixed, sectioned and stained at intervals of 12 hours, it is found by plotting the average length of the pollen tubes in each pistil against time in 12 hour periods that the growth curve of selfed pollen tubes is a straight line which reaches less than half the distance to the

ovary during the life of the flower, while the curve of crossed pollen tubes resembles that of an autocatalysis and reaches the ovary in less than 96 hours. Further, it is unnecessary to know why gametes, which themselves bear various factors effective on the behavior of self-sterile plants, should act during the process preliminary to fertilization as if each bore the factors characteristic of the plant on which they were produced. Attention is called, however, to the fact that modern discoveries tend more and more to show that the sole function of the gametophytes of the Angiosperms is to produce sporophytes. The characters which they possess appear to be wholly sporophytic, the factors which they carry functioning only *after* fertilization. In other words, the hereditary genes carried by pollen grains—and probably by eggcells—may be thought of as being dormant until the appropriate time comes for them to play their proper parts.

It may be helpful to draw a picture of what may be expected to happen under the assumptions which have been made and to see how closely the actual facts are paralleled. First, it should be stated that no interpretation of the fact that within a family the intra-sterile classes are often of unequal size can be made without assuming linkage except by a number of awkward subsidiary assumptions. Second, our picture is as simple as possible in view of the facts at hand, but it may be extended *ad libitum* as far as number of factors is concerned. Third, since all of the facts of Mendelism are merely those to be expected from the known behavior of the chromosomes as carrying bodies for our hypothetical genes, chromosome diagrams are used without apology.

Assume first then that a plant of *N. Forgetiana* is heterozygous for 3 linked factors effective on the behavior of self-sterile plants, and that the homologous chromosomes of an *N. alata* plant are heterozygous for different multiple allelomorphs of the same factors. The two plants may be represented thus.



These plants cannot be self-fertilized because all of their gametes are influenced by their sporophytic constitution $ABC.A'B'C'$ and $A''B''C''$. $A'''B'''C'''$, respectively, nor can either be fertilized by gametes borne on a plant of like constitution.

Now each of these plants of *N. Forgetiana* and of *N. alata* produces 8 types of gametes. *N. Forgetiana*, for example, produces great numbers of ABC and $A'B'C'$, medium numbers of $A'BC$, $AB'C'$, ABC' and $A'B'C$ by one crossover or linkage break, and small numbers of $AB'C$ and $A'BC'$ by double crossing over. *N. alata* behaves in a similar manner. Thus the progeny of this cross will consist of $8^2 = 64$ intra-sterile, inter-fertile groups of individuals, the groups being of various sizes. Further, since no individuals with constitutions $ABC.A'B'C'$ or $A''B''C''$. $A'''B'''C'''$ are produced in the F_1 generation, every F_1 class will be fertile with both of its parents.

Since by hypothesis two plants need differ by but one effective factor in order to be fertile in inter-crosses, it is clear that matings may occur in which certain of these factors are homozygous. To illustrate, it is possible to obtain two plants of constitutions $ABC.A'B'C'$ and $A''B''C$. $A'''B'''C$ among the grandchildren of this generation. The factor C is homozygous and can be left out of consideration since the two plants form only 4 different types of gametes each. The first forms gametes AB and $A'B'$ in large numbers, and $A'B$ and AB' in small numbers; likewise the second forms gametes $A''B''$ and $A'''B'''$ in large numbers, and $A''B'''$ and $A'''B''$ in small numbers. Even with the elimination of the C allelomorphs as effective differences, therefore, it is possible to obtain a family having 16 intra-sterile classes by crossing two such plants. Of these classes 4 will be large, 8 medium and 4 small.

It is not unlikely that 16 classes is the maximum that need be considered, but what of the smaller number of groups usually found? The answer is that simplification can go on and on until very few intra-sterile classes are formed.

Suppose, for example, that $AB.AB'$ is crossed with $AB.A'B$; 4 classes will be formed $AB.AB$, $AB.A'B$, $AB'.AB$ and $AB'.A'B$, of which the third class will be sterile with the female parent and the second class sterile with the male parent. Or, suppose that AA' is crossed with AA'' . Again 4 classes will be formed, AA , AA' , AA'' and $A'A''$. AA may then be crossed with AA' , and only 2 intra-sterile classes formed.

This may be assumed to be the simplest form in which a natural population of self-sterile plants may exist, but theoretically it is possible by taking advantage of the phenomenon of pseudo self-fertility or pseudo

cross-fertility to obtain a family consisting of but 1 group. In such a family every plant would be sterile with every other plant. It is possible that the two families met in the course of our experiments in which cross-sterility appeared to be universal, were of this kind.

This hypothesis fits perfectly what to us seem the important experimental facts. One may have F_1 generations of various types of complexity, with an increasing simplicity in succeeding generations through inbreeding; or, the F_1 generation may be less complex than the F_2 generation,—the effect of inbreeding first becoming apparent in the F_3 generation. Cross-sterility with resultant intra-sterile classes in single or in different families is explained. Both sterility and fertility in back-crosses is clear. The similar behavior of reciprocal crosses is reasonable. Perfect intra-sterility in the asexual progeny of a self-sterile plant is what is to be expected. The facts established by DARWIN and by CORRENS when viewed with due consideration for pseudo-fertility become orderly. And yet this is but hypothesis, to be modified, extended, restricted or superseded as becomes necessary. If it proves useful for a time it will have served its purpose. Even now there are points upon which other heredity phenomena throw no light. We will devote a concluding paragraph to their discussion.

In our experimental work the number of intra-sterile classes and the number of individuals within each class were determined as definitely as possible. But these experiments have been too much of the pioneer type not to be rough in many ways. With our present experience the same facts could be determined more accurately and on much larger populations with less work than the original determinations demanded, and this appears to be a requisite for further advance. According to our hypothesis, accepting it without subsidiary refinements, the number of classes should always be even, and the classes should be equal in size when only 2 or 4 make up the population. Furthermore there should always be pairs of classes containing the same number of individuals. Now in making some of our calculations we have assumed that the individuals are distributed within the classes in numbers corresponding to the frequencies of the point binomial. Such a distribution was assumed only as a limiting type of unequal grouping, however, there being scarcely any evidence that such a distribution is characteristic. As a matter of fact only in the F_1 of cross No. 2 and No. 3 and its descendants, families H and I, is it possible to say that the number of individuals within the various classes may not be approximately equal. But in these cases we

stumble upon an obstacle that cannot be cleared away with our present knowledge. The distributions found in these families are such that larger samples of the populations could not give us classes of equal size. For the present we must accept the conception of a small number of intra-sterile groups in certain families with all that this involves. We might explain them by subsidiary hypotheses of differential vitality or by reduplication in the sense of BATESON, but since there is no other good reason for such assumptions we prefer to leave these matters in abeyance.

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